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ACCESSORY BONES
OF THE
HUMAN FOOT



ON COMMISSION TO EINAR MUNKSGAARD
COPENHAGEN 1948

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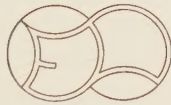
ACCESSORY BONES OF
THE HUMAN FOOT

Translated from the Danish
by
ELISABETH AAGESEN.

DYRE TROLLE

ACCESSORY BONES OF THE HUMAN FOOT

A RADIOLOGICAL, HISTO-EMBRYOLOGICAL,
COMPARATIVE -ANATOMICAL, AND GENETIC STUDY



ON COMMISSION TO EINAR MUNKSGAARD
COPENHAGEN 1948

*Denne Afhandling er af det lægevidenskabelige Fakultet
antaget til offentligt at forsvares for den
medicinske Doktorgrad.*

København, den 15. December 1947.

K. A. Jensen,
h. a. dec.

PREFACE

The idea of the present investigation suggested itself to me after observation of an isolated minor fracture of the cuboid in a patient from the *Usserød Sygehus*. This finding gave rise to a discussion on the question of accessory bones, which made me interested in these bones. After having mentioned the finding to Physician-in-Chief *Chr. I. Baastrup* and Physician-in-Chief *Niels Lauge Hansen*, M.D., then assistant physician, I was stimulated to a further study of the subject. Finally, subsequent conversations with the late Professor *C. M. Steenberg*, Ph. D., and with Professor *Harald Okkels*, M.D., prompted me to attempt an elucidation of the genesis of the accessory bones.

The radiographs of the present work are derived from the X-Ray Department, *Bispebjerg Hospital* (Physician-in-Chief *Chr. I. Baastrup*), the X-Ray Department of the *Finsen Institute* (Physician-in-Chief *Børge Worning*, Ph. D.), *Ortopædisk Hospital*, Copenhagen (Physician-in-Chief *Poul Guildal*), and *Ortopædisk Hospital*, Aarhus (Physician-in-Chief *P. G. K. Bentzon*, M.D.). Moreover, the *Finsen Institute* allowed me to have reproductions made of my X-ray films in its photographic studio (Miss *L. Bech*).

The embryos have been collected by the respective nurses from patients admitted for spontaneous or induced abortion to the *Bispebjerg Hospital* (Professor *Harald Abrahamsen*, M.D., Professor *Jens Foged*, M.D., and Professor *Einar Thomsen*, M.D.), the *Kommunehospital* (Professor *Otto Mikkelsen*, M.D., and Surgeon-in-Chief *Torben Knudtzon*, M.D.), *Københavns Amtssygehus*, *Gentofte* (Professor *Poul Morville*, M.D.), *Næstved Amtssygehus* (Surgeon-in-Chief *Hans Tønnesen*, M.D.), the *Rigshospital* (Professor *Ebbe Brandstrup*, M.D. and Professor

J. Engelbreth-Holm, M.D.), and the *Usserød Sygehus* (former Surgeon-in-Chief *Ch. E. Hindborg*).

The preparatory treatment of sections for microscopical examination was taught me in the Histo-Embryological Department, University of Copenhagen, under the leadership of the late Professor *C. M. Steenberg, Ph. D.* and *P. Holst Christensen, Ph. D.* Later I had occasion to carry out this manual work in that same Department and in the laboratory of *Københavns Militærhospital (H. Seemann, M.D.)*, aided by various assistants, in the first instance by Miss *Gerda Hvidemark*, Mr. *Nielsen*, and Mr. *Meyer*. The expenses to this assistance were in part defrayed through grants from *P. Carl Pedersens Fond*.

During the routine manual work *P. Holst Christensen, Ph. D.* assisted me with the constantly arising minor problems within the technique. Dr. *Holst Christensen* has also been so kind as to look over my list of animal synonyms.

Mrs. *Grethe Hanson* has with great interest and readiness assisted me with the proof-reading.

My sincerest thanks are due to all who have thus contributed to the carrying through of the work, and to all the institutions mentioned above.

The histological examinations as well as the analysation and arrangement of my material were carried out in my home. I shall here take the opportunity to thank also my wife, Dr. *Elli Trolle*, for all her aid, among others by discussing different problems with me. In return for this aid and for her encouragement and understanding during my often laborious work as well as for the support she has given me I want to *dedicate this book to my wife.*

The manuscript was given in to the Faculty of Medicine, University of Copenhagen, on February 6, 1947.

Copenhagen, April 1948,

Dyre Trolle.

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ABBREVIATIONS

- a: astragalus.
cI, II, III: os cuneiforme I, II, and III.
c₁, 2, 3, 4: centrale 1, 2, 3, and 4.
ca: calcaneus.
calc. acc: calcaneus accessorius.
calc. bip: calcaneus bipartitum.
cd₁, 2, etc.: centrale distale 1, 2, etc.
cfd: centrale fibulare distale.
cfp: centrale fibulare proximale.
CH: crown heel length.
cp = cpr: centrale proximale.
cph: centrale prehallucis.
CR: crown rump length.
ctd: centrale tibiale distale.
ctp: centrale tibiale proximale.
cub: os cuboideum.
cunI, II, III: os cuneiforme I, II, and III.
D: right foot.
d: digitus.
F: fibula.
f: fibulare.
Fe: femur.
i₁, 2, etc.: intermedium 1, 2, etc.
int: os intermetatarsale I.
intph: os interphalangeale.
mtI, II, etc.: os metatarsale I, II, etc.
mtph: os metatarsale prehallucis.
nav: os naviculare.
paracun: os paracuneiforme.
per: os peroneum.
ph: prehallux.
pi: pisiforme.
pm: postminimus.
S: left foot.

sI, II, etc.: os sesamoideum metatarso-phalangeale I, II, etc.
 sIm: os sesamoideum metatarso-phalangeale mesiale.
 siI: os sesamoideum interphalangeale hallucis.
 siIp: os sesamoideum partitum interphalangeale hallucis.
 sipV: os sesamoideum interphalangeale proximale dig. V.
 T: tibia.
 t: tibiale.
 t₁, 2, etc.: tarsale distale 1, 2, etc.
 ta: talus.
 td₀: tarsale distale prehallucis.
 td₁, 2, etc.: tarsale distale 1, 2, etc.
 tib: os tibiale.
 tph: tarsale prehallucis.
 tpm: tarsale postminimus.
 tp₀: tarsale proximale prehallucis.
 tp₁, 2, etc.: tarsale proximale 1, 2, etc.
 tr: os trigonum.
 y: centrale prehallucis.
 I, II, etc.: os metatarsale I, II, etc.
 1, 2, 3, etc.: number of phalanges to each digitus.
 .: os sesamoideum metatarso-phalangeale et interphalangeale.
 ♀: female
 ♂: male.
 o: sex unknown.
 BBH: *Bispebjerg Hospital*, Copenhagen.
 FI: *Finseninstitutet*, Copenhagen.
 OHK: *Ortopædisk Hospital*, Copenhagen.
 OHA: *Ortopædisk Hospital*, Aarhus.

LIST OF ANIMALS

<i>aepyprymnus rufescens</i>	red kangaroo-rat	rod kængurorotte
<i>agama colonorum</i>	agam	agam
<i>amblystoma tigrinum</i>	salamander (metamorphosed axolotl)	landsalamander (forvandet axolotl)
<i>anas boscas</i> var. <i>domesticus</i>	domestic duck	husand
<i>ascalabotes fascicularis</i>	gecko	gekko
<i>blarina brevicaudata</i>	short-tailed shrew	korthalet spidsmus
<i>bombinator igneus</i>	fire-bellied toad	klokkefro
<i>bos</i>	ox	oxe
<i>bos taurus</i>	domestic ox	tamoxe
<i>bradypus tridactylus</i>	three-toed sloth	trefingret dovendyr
<i>bufo variabilis</i>	green toad	tudse
<i>caiman crocodilus</i>	caiman	alligator
<i>caiman latirostris</i>	caiman	alligator
<i>camelus</i>	camel	kamel
<i>canis familiaris</i>	domestic dog	tamhund
<i>cavia cobaya</i>	guinea-pig	marsvin (gnaver)
<i>cavia porcellus</i> L.	guinea-pig	marsvin (gnaver)
<i>centetes ecaudatus</i>	tenrec (insectivore)	tenrek, børstesvin (insektæder)
<i>cervus capreolus</i>	roe-deer	raadyr
<i>chelonina mydas</i>	edible turtle	spiselig havskildpadde
<i>choloepus didactylus</i>	two-toed sloth	tofigret dovendyr
<i>chrysemys marginata</i>	tortoise	prydschildpadde
<i>citellus citellus</i> L.	ground squirrel	jordegern
<i>condylura cristata</i>	star-nosed mole	stjernemuldvarp
<i>crocodilus biporcatus</i>	crocodile	krøkodille
<i>crocodilus niloticus</i>	Nilotic crocodile	nilkrøkodille
<i>cryptobranchus japonicus</i>	Japanese giant salamander	japansk kæmpesalamander

<i>dasypus hybridus</i> Desm.	seven-banded armadillo	syvbæltet bæltedyr
<i>dasyurus viverrinus</i>	dasiure	pungmaar
<i>didelphis marsupialis</i> L.	marsupial possum	pungrotte
<i>didelphys murina</i>	marsupial possum	pungrotte
<i>didelphys quica</i>	marsupial possum	pungrotte
<i>didelphys virginiana</i>	Virginian opossum	pungrotte
<i>dromiceus novaehollandiae</i>	emu	emu
<i>echidna hystrix</i>	Australian anteater	myrepindsvin
<i>elephas africanus</i>	African elephant	afrikansk elefant
<i>emys lutaria</i>	pond tortoise	sumpskildpadde
<i>equus</i>	horse	hest
<i>erethizon dorsatus</i> <i>epixanthus</i>	tree porcupine	træpindsvin
<i>erinaceus europaeus</i> L.	hedge-hog	pindsvin
<i>felis catus</i>	house cat	huskat
<i>gallus bankiva</i> var. <i>domesticus</i>	domestic hen	gaardhøne
<i>halmaturus</i>	wallaby	kænguru
<i>hatteria</i>	New Zealand lizard	New Zeelandsk øgle
<i>hemisentetes semispinosus</i> Cuv.	demitenrec (insectivore)	halvtænrek, børstesvin (insektæder)
<i>hyla arborea</i>	tree frog	løvfrø
<i>hylobates</i>	gibbon	gibbon
<i>hynobius retardatus</i>	Japanese salamander species	japansk salamanderart
<i>hyrax syriacus</i>	Syrian coney	syrisk klippegrævling
<i>lacerta muralis</i>	emerald-lizard	smaragdfirben
<i>lama vicugna</i>	vicuna	vicunja
<i>larus canus</i>	common gull	stormmaage
<i>lepus cuniculus</i>	rabbit	kanin
<i>leucodon araneus</i> L.	ordinary shrewmouse	almindelig spidsmus
<i>lutra</i>	otter	odder
<i>manis previcaudatus</i>	manis	skældyr
<i>manis tricuspis</i>	manis	skældyr
<i>microcebus myoxinus</i> Ptrs.	dwarf maki	dværgmaki
<i>molossus spec.</i>	bat	buldogflagermus
<i>mus decumanus</i>	brown rat	brun rotte
<i>mus musculus</i> L.	house mouse	husmus
<i>mus rattus</i>	black rat	sort rotte
<i>mustela vulgaris</i>	weasel	brud

ornithorynchus	duckbilled platypus	næbdyr
ovis	sheep	faar
pelobates fuscus	garlic-toad	løgfrø
phalangista Cookii	phalanger	pungabe
phascolarctos cinereus	grey koala	graa pungbjørn
ploceus	weaverbird	væverfugl
procavia daemon	rock coney	klippegrævling
putorius ermineus	ermine	hermelin
rana temporaria	brown frog	butsnudet frø
ranidens sibiricus	primitive newt	primitiv halepadde
salamandrella kayserlin- gii	primitive newt	primitiv halepadde
salamandra maculosa	spotted salamander	landsalamander
scalops aquaticus	North American mole	nordamerikansk muld- varp
scalops argentatus	North American mole	nordamerikansk muld- varp
sciurus vulgaris L.	squirrel	egern
seps chalcides	snake-shaped lizard	snogeøgle
siredon pisciformis	axolotl	axolotl
sorex vulgaris	ordinary shrew	almindelige spidsmus
sternotherus	African tortoise	afrikansk skildpadde
sus	genus hog	svine-slægten
sus scropha dom. L.	domestic hog	tamsvin
talpa europaea	common mole	muldvarp
tarsius spectrum L.	tarsius	spøgelsesabe
tatusia hybrida	seven-banded armadillo	syvbæltet bæltedyr
tatusia novemcinctus	nine-banded armadillo	nibæltet bæltedyr
testudo graeca	Greek tortoise	græsk landskildpadde
triton cristatus	crested newt	stor vandsalamander
ursus arctos	brown common bear	brun landbjørn
xenopus laevis	clawed toad	klofrø

INTRODUCTION

Experience has shown that little is known of the accessory bones in the human foot, although these bones by no means are rare curiosities of no practical importance. On the contrary, the accessory bones are of frequent occurrence, being ascertainable radiographically in 3 out of 4 humans (*Burman & Lapidus* 1931), in other words in 75 per cent. *Geist* 1914 found the accessory bones in and about the tarsus alone in 30 per cent. In addition these bones are of practical clinical interest, partly because of their importance from the point of view of differential diagnosis, particularly as regards differentiation from fractures, and partly because some of them may give rise to symptoms.

No systematic analysis of the accessory bones has been made since the end of the 19th century, although such would seem highly necessary, because to-day — thanks to the extensive use of radiography — we know a far greater number of accessory bones than was the case in the nineties. Various radiological statistical works (see later) have, indeed, been published within the past few decades; but they deal with the frequency of the most common accessory bones only. The rarer ones are not mentioned. The latter, on the other hand, are found described in numerous casuistic reports.

Hence the comprehensive review of all the accessory bones in the foot given in the present work seems highly appropriate.

The question of the genesis of the accessory bones is still a subject for discussion. Within the last decade of the 19th century, when only a small proportion of the now familiar accessory bones were known to exist, most writers, in the first instance *Bardeleben*, *Pfitzner*, and *Thilenius*, took the accessory bones to be phylogenetic formations. This hypothesis seemed to have been borne out by the facts that some of these bones had been demonstrated histo-embryologically in man (in the case of the hand *Thilenius* 1894 and 1896 even demonstrated the presence of most of them), and that several bones corresponding to the accessory bones had been found within the animal world. *Emery* 1894—1897, however, holds a somewhat different view. This writer divides the accessory bones preformed in hyaline cartilage in 3 groups: 1) occur only in a single

animal species or animal family, 2) are typical of a whole class of animals, and 3) are traceable through the entire animal kingdom, being, in other words, elements in the primitive foot. Investigations into this problem have not since been resumed on a large scale, but many subsequent writers — even up to modern times — have accepted the theory of a phylogenetic genesis on the basis of the already existing investigations.

As mentioned above, *Emery* raised moderate objections to the theory of a decidedly phylogenetic genesis, but also others objected, and even more strongly so. Thus, *Tornier* 1891 and 1894, particularly stated that the occurrence of accessory bones is due to ossification of tendons and ligaments developed in the individual cases in consequence of pressure and traction. Various subsequent writers (a. o. *Retterer & Lelièvre* 1911, *Retterer* 1920, *Lunghetti* 1909, *Weidenreich* 1923, and *Güntz* 1942) arrived at similar results with regard to the few accessory bones they investigated. This theory is, moreover, supported by the fact that the frequency of certain accessory bones increases with increasing age. The above views gain ground gradually as our knowledge of secondary and pathological ossification becomes more extensive.

The accessory bones in the foot have now proved to be so numerous that far from all of them can be accounted for on the basis of the number of elements found, according to our present knowledge, in the primitive tetrapod foot. It has, therefore, been thought a matter of interest to test — on a larger scale — the previous histo-embryological investigations to see whether bones preformed in hyaline cartilage do exist at all. This testing will be the main subject of the work here presented.

In addition, histo-embryological findings from a number of vertebrates will be reviewed, and the evolution from the primitive tetrapod foot discussed. It will then be possible to see which accessory bones may be conceived to originate from elements of the primitive tetrapod foot.

Even though a certain proportion of the accessory bones may be accounted for on a phylogenetic basis, there will — according to what has been stated above — still be a great number left whose existence cannot be explained on this basis. Accordingly various other possibilities of origin will be discussed as well, including the secondary and the pathological ossifications.

Chapter 1.

ACCESSORY BONES OF THE HUMAN FOOT

The normal human foot is constructed of the following constant bones: 7 tarsal bones, 5 metatarsals, 14 phalanges, and 2 sesamoid bones situated in close relationship to the proximal phalanx of the big toe.

A definition of what should be understood by accessory bones¹⁾ does not exist. I have given the following definition:

Accessory bones are all inconstant, independent, well-defined bones — in an otherwise normally developed foot — the existence of which is not due to a recent minor fracture²⁾ or other definitely pathological condition, no matter whether these bones bear no, or a less or more intimate relationship to the constant bones, or entirely replace them because of a division of the latter into several segments. Accessory bones may be found practically anywhere in the foot.

It is a wide-ranging definition, but, as will appear from the present work, this cannot be otherwise. The fact that the recent minor fractures and other definitely pathological conditions are excepted from the category of accessory bones is due to the practical-clinical importance of the lesions.

This chapter has been divided in 3 sections for the sake of perspicuity:

- I. Drawings of feet.
- II. Frequency Table.
- III. Brief description of the individual accessory bones attended by radiographs.

¹⁾ By others called inconstant or supernumerary bones.

²⁾ By a minor fracture I understand such a fracture as gives rise to the formation of a peripheral, up to ab. hazel-nut-sized detached element. The fracture will thus generally involve only a small part of the bone, but exceptions do occur, e. g. transverse fracture of a sesamoid bone.

I. *DRAWINGS OF FEET*

Explanation to Figure 1.

1. calcaneus accessorius.
2. calcaneus secundarius.
3. os aponeurosis plantaris.
4. os cuboideum secundarium.
5. os cuneiforme I bipartitum.
6. os cuneo-metatarsale I plantare.
7. os cuneo-metatarsale I tibiale.
8. os cuneo-metatarsale II dorsale.
9. os in sinu tarsi.
10. os intercuneiforme.
11. os intermetatarsale I.
12. os intermetatarsale IV.
13. os interphalangeale.
14. os naviculare bipartitum.
15. os naviculo-cuneiforme I dorsale.
16. os paracuneiforme.
17. os peroneum.
18. os retinaculi.
19. os sesamoideum interphalangeale.
20. os sesamoideum metatarso-phalangeale.
21. os sesamoideum partitum interphalangeale et metatarso-phalangeale.
22. os subfibulare.
23. os subtibiale.
24. os supertalare.
25. os sustentaculi proprium.
26. os talo-calcaneare posterior.
27. os talo-naviculare dorsale.
28. os talo-tibiale dorsale.
29. os tendinis Achillis.
30. os tibiale.
31. os trigonum.
32. os trochleae.
33. os tuberis calcanei.
34. os unci.
35. os Vesalianum.

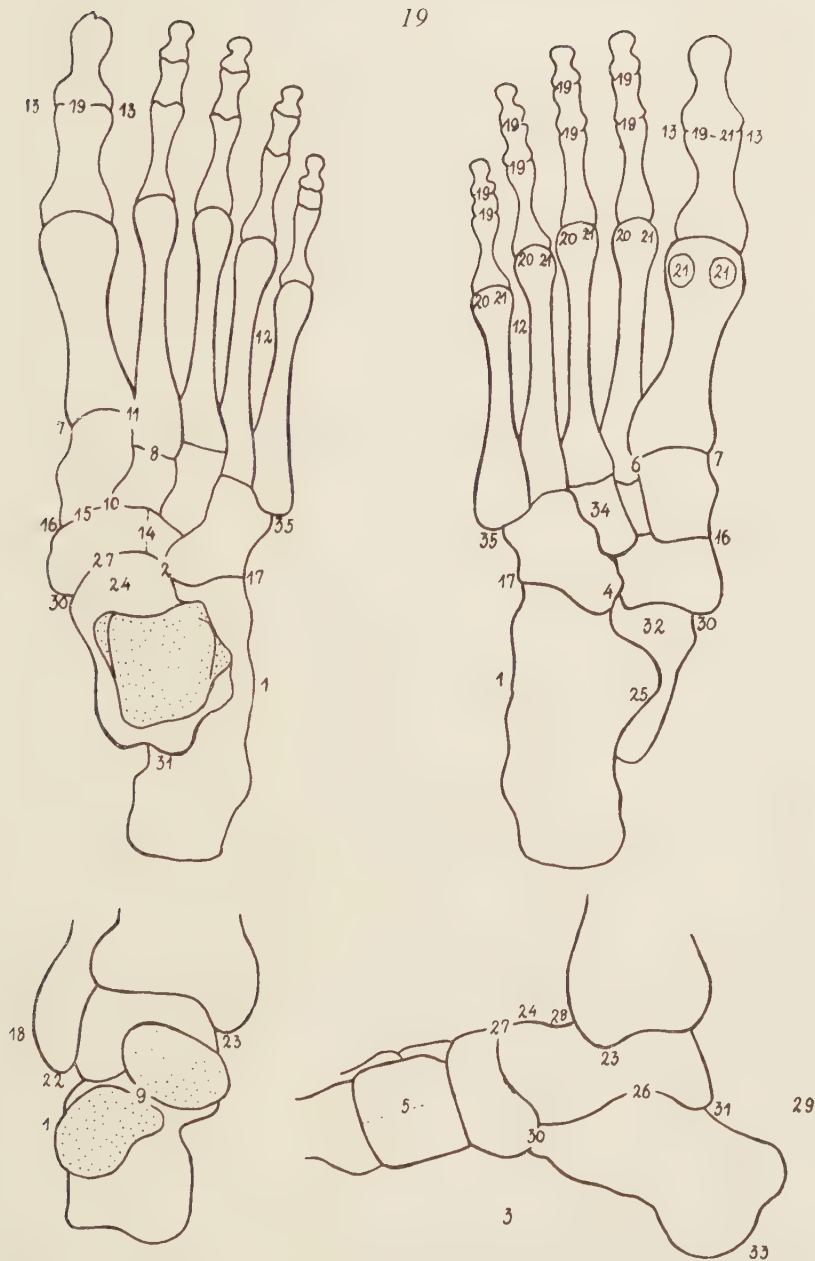


Fig. 1 shows the sites of the accessory bones in the present work.

Be it emphasized that the list of accessory bones is not complete, but comprises only the most common ones and such rare ones as I have found, partly in the literature and partly personally.

II. FREQUENCY TABLE WITH Incidence table with

investigator year X-ray—anatom. number	ARHO BIZARRO 1940 X-ray 1074	1920-21 X-ray 100	GEIST 1914 X-ray 100	GRUBER 1877, 1885 anatom ()	HEIMER- ZHEIM 1925 X-ray 1800	HOLLE 1938 X-ray 1000	LEIM- BACH 1938 X-ray 500
calcaneus accessorius							
calcaneus secundarius	1	1	2		0.1	1.7	0.4
os cuneiforme I bipar- titum				0.33 (2574)			
os intermetatarsale I	0.3			8	0.4	6.8	
os interphalangeale os paracuneiforme							
os peroneum	8.3	5	7		2.3	9.5	2.8
os sesamoideum inter- phalangeale							
d I	10	5				4.3	
d I dorsale						0.7	
prox d II		1					
dist d II						0.8	
prox d III		1					
dist d III		1					
prox d V							
dist d V						0.7	
os sesamoideum metatar- so-phalangeale							
II t — f	2	1				5.4-0.7	
III t — f						0.7-0.4	
IV t — f		2				1.8-0	
V t — f	20-4	10				13.3-2.0	
os sesamoideum partitum							
interphalangeale d I						0.1	
metatarso-phal. I t-f		4-0	16			14.3-2.5	
metatarso-phal. V t-f						0.1-0	
os subfibulare							0.2
os subtibiale	0.7					1.2	0.2
os sustentaculi proprium						1.5	
os talo-naviculare dorsale	0.1	1			0.7	0.97	1.6
os tibiale	6.4	2	14		1.2	7.9	3.6
os trigonum							
	4.6	7	7		4.3	12.7	4.6
os Vesalianum	*			0.3 (2127)	0.9	0	

ENDING DISCUSSION

centage indications

ZNER e, 1896 atom)					Own histo- embryolo- gical exa- minations	
					feet 500	pairs of feet 250
					0.6	0.8
(520)					0	0
(840)						
(425)					2.4	2.4
(840)						
(425)	FABER 1934	HASSELWANDER 1910	TOKMAKOFF 1928-29		6.8	8.0
(520)	X-ray (1000) 1.2	anat. (110) 10	anat. (100) 14			
					1.9	2.7
					13.2	13.2
(425)	LUNGHETTI 1909					
(520)	hist. (138) 16.8				0.4	0.4
(385)	KASSATKIN 1934					
	X-ray + anat, 770					
0.6	54.8				56.0	57.8
0					0	0
0					0	0
0.8					0	0
0					0	0
0					0	0
0					9.1	9.6
0					0	0
(385)		MAYR 1935				
		X-ray, 470				
8 - 0	4.2 - 0.2	4 - 0			4.0	4.3
- 0	0.7 - 0	0.4 - 0			0.5	1.1
- 0	1.4 - 0.6	1.7 - 0			2.7	2.7
5 - 6.2	12.2 - 10.1	9 - 1.9			26.2	26.2
	KEWENTER 1936	BURMAN & LAPIDUS 1931	INGE & FERGUSON 1933	WOLF 1912		
	X-ray, (800)	X-ray, (1000)	X-ray, (678) *	X-ray, (900)	1.8	2.7
0					0	0
- 0.26	33.5 (91.4-3.7)	7.2 - 0.6	9.2	6 (94.4 - 5.6)	0	0
- 0					0	0
					0.2	0.4
					0	0
(425)					0	0
(425)	SCHRODER 1931					
(520)	X-ray, (2000) 0.5				0	0
(425)	LUNGHETTI 1909				6.4	7.6
(520)	hist, (160) > 12.5					
(378)	STIEDA 1889				0	0
(520)	anat, (305) 5.9				0	0
(520)					0	0

ected by me to comprising only persons over 20 years of age.

As appears from the Table, the figures indicating the percentage frequency of one and the same accessory bone often vary considerably from one investigator to the other. This may in some measure be due to accidental circumstances and may, therefore, be explained statistically, since the number of feet examined always is rather small in proportion to the frequency of the accessory bones (notably, of course, where the rare bones are concerned). The results arrived at may, however, depend also on other factors, such as the accuracy of the method applied and the solicitude of the individual investigator.

Information on the frequency of accessory bones is most easily obtained by radiography, which is also the most commonly applied method. This method consists in collecting — according to one's energy — so and so many pictures of feet, inspect them, and note down how often accessory bones are found. The percentage incidence is then easily calculated. Many objections may be raised to such a procedure. Generally pictures of the individual foot are available from 1, or perhaps 2 aspects only. Hence many accessory bones are not visible at all, while the presence of others is doubtful. It must then be a matter of opinion whether the latter are to be included or not. Correspondingly, irrelevant formations (e. g. minor fractures) may become included, although repeated X-ray examination with special radiographs would have disclosed the facts. The X-rays applied are often too hard, penetrating through many of the delicate accessory bones, which are then only just visible or not visible at all.

One of the few writers who have taken radiographs with accessory bones in mind is *Kewenter* 1936 in his investigations into the presence of a division of the 2 constant sesamoid bones of the big toe. He took pictures from 3 aspects and obtained thereby a percentage frequency far exceeding that found by other investigators.

The 4 most commonly applied aspects and foot positions are as follows (according to *Clark* 1938):

1. Dorsi-plantar view, with the sole of the slightly plantarly flexed foot resting direct on the plate: centre with vertical tube over the cubo-navicular articulation.

2. Dorsi-plantar oblique view, same position as before, only the knee is directed tibially, so that the crus makes an angle

of 20 to 30 degrees with the vertical. Centre over the cubo-navicular articulation, but in such a manner that the central ray is at right angles to the dorsal surface in this place.

3. Fibular (or tibial) lateral view, with the fibular (or the tibial) border of the foot resting on the plate, while the sole of the foot makes a right angle with the plate. Centre with vertical tube over the naviculo-cuneiform I articulation.

4. Lateral oblique view, with the entire outside of the crus resting on the underlayer. In this position the fibulo-dorsal part of the foot rests on the plate, while the sole makes an angle of nearly 45 degrees with the plate. Centre with vertical tube over the base of the fifth metatarsal bone.

Müller 1925 added a fifth view, the tangential, (that applied by *Kewenter* 1936) for examination of the sesamoid bones of the big toe: The patient lies prone resting his knees on the underlayer, while the toes with hyperextended proximal joints rest on the plate. The central ray is directed towards the sesamoid bones, making an angle of ab. 30 degrees with the sole.

Another method of getting information on the frequency of accessory bones is the anatomical. The result can here be relied upon only if the investigation is made with this special object in view, if a careful dissection is carried out followed by maceration, according to *Teichmann*, and if the investigation is undertaken by a skilled and attentive observer. *Pfitzner* repeatedly showed — 1891, 1892, 1895, and 1896 — how different the results arrived at may be, dependent on the importance attached to the above conditions.

Such an anatomical investigation strictly carried through on a great number of feet is an extremely time-stealing and troublesome work, which has actually been done only by *Pfitzner* — 1892 and 1896. He personally examined 425 feet and conducted corresponding examinations of further 416 feet, all belonging to individuals from 13 years of age upwards.

A short cut may be made by combining the radiographic and the anatomic methods. By X-ray visualisation it is possible first to separate off the feet which have or are suspicious of having accessory bones. Afterwards, at the anatomical examinations of these feet, one can at once incise at the site or sites of these supposed accessory bones. *Hasselwander* 1903 has to some extent entertained this idea.

III. BRIEF DESCRIPTION OF THE INDIVIDUAL ACCESSORY BONES ATTENDED BY RADIOGRAPHS

A brief review of the accessory bones will be given in the following for the sake of orientation. A detailed account of anatomical conditions will be omitted, partly because such have been published in the literature (in the first instance by *Gruber* and *Pfitzner*), and partly because I have got no own material for such an anatomical investigation.

A brief description will be given of each individual accessory bone followed by a radiograph and/or a diagram of the bone concerned. There are various reasons why I have preferred picturing of radiographic findings to anatomic. First, I have an own radiographic material¹⁾, but no anatomic; secondly, the radiographic findings are the most interesting from a clinical point of view; and thirdly, most of the accessory bones are recognized radiographically. In the cases where I have no radiographs at my disposal (neither own nor from others) I have availed myself of the anatomic diagrams (from the literature). The number of accessory bones in each individual case has not been settled, because the feet have not been submitted to thorough radiographic examination with a view to this question.

For each accessory bone its discoverer is mentioned, where possible, and reference is made, after the description, to the investigators who have studied the bone in question. The literature on the individual bones is generally exceedingly rich, so it has been impossible to include all the writers, but I hope at least to have mentioned the most important.

The numeration corresponds to that in Fig. 1, where the accessory bones are mentioned in alphabetic order.

1. *Calcaneus accessorius* (*Pfitzner* 1896).

The calcaneus accessorius is situated just off the trochlear process of the calcaneum, in other words on the fibular side of this bone under the fibular malleolus. When biggest it is hardly the size of a pea. It is difficult to discern in a radio-

¹⁾ That female feet are in the majority in the present material is no doubt due to the fact that at least two-thirds of the patients in the *Bispebjerg Hospital* (from which most of the material is derived) are women.

graph, but one may succeed by radiographing the hyper-extended foot with the foot sole resting on the plate.

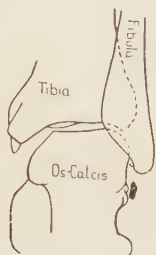


Fig. 2. (After Holland 1928).

References: *Francillon* 1932, 1934, *Hasselwander* 1910, *Holland* 1928, *Pfitzner* 1896.

2. *Calcaneus secundarius* (*Stieda* 1869).

The calcaneus secundarius lies in the interspace between calcaneum, talus, cuboid, and navicular. The bone is generally roundish and may reach the size of a large coffee berry. Radiographically it is plainly visible from the lateral oblique aspect.

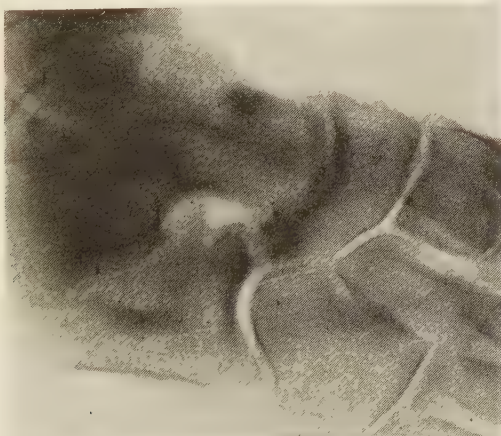


Fig. 3. Female, aged 23, unilateral finding (OHA).

References: *Arho* 1940, *Bierman* 1922, *Bizarro* 1920—1921, *Burman & Lapidus* 1931, *Dwight* 1902, 1910, *Francillon* 1934, *Geist* 1914, *Gruber* 1871, *Hasselwander* 1910, *Heimerzheim* 1925, *Hohmann* 1934, *Holland* 1928, *Holle* 1938, *Krida* 1923, *Leimbach* 1938, *Lilienfeld* 1907, *Loyer* 1920, *Mercer* 1931—1932, *Pfitzner* 1896, *Stieda* 1869, *Tornier* 1894, *Watkins* 1937.

3. *Os aponeurosis plantaris.*

The os aponeurosis plantaris lies inclosed in the plantar aponeurosis, in greater or smaller proximity to the point of origin of the aponeurosis on the tuber calcanei. The bone is oblong and flat. It varies greatly in size. Radiographically it is best seen from the lateral or the lateral oblique aspect.



Fig. 4. Male, aged 58, bilateral finding (BBH.).

References: Güntz 1942, Harris 1933.

4. *Os cuboideum secundarium* (Schwalbe 1898).

The site of the os cuboideum secundarium is on the plantar side at the point of contact between cuboid, navicular, talus, and calcaneum. The bone may reach the size of a hazel nut. Radiographically it is visible both in dorsi-plantar and lateral oblique views, but it is impossible to say for certain whether it is entirely independent.



Fig. 5. (After Dwight 1910). Male, aged 44, left foot (right the same, but synostosis to the cuboid).

References: *Bierman* 1922, *Dwight* 1910, *Holland* 1928, *Pfitzner* 1896, *Schwalbe* 1898, *Tornier* 1894, *Volkov* 1902, *Watkins* 1937, *Zimmer* 1938.

5. *Os cuneiforme I bipartitum* (*Morel* 1757).

As appears from the name, *os cuneiforme I bipartitum*, there is found a bipartite, tibial cuneiform. The bipartition consists in the reported cases in the formation of a dorsal and a plantar bone, of which the former generally is the bigger. The bipartition is difficult to discern in a radiograph, but one may succeed both from the lateral aspect with the tibial border of the foot resting on the plate, and from the dorsi-plantar aspect (see also Fig. 20, p. 34).



Fig. 6. (After *Pfitzner* 1896). Adult male, only right foot examined.

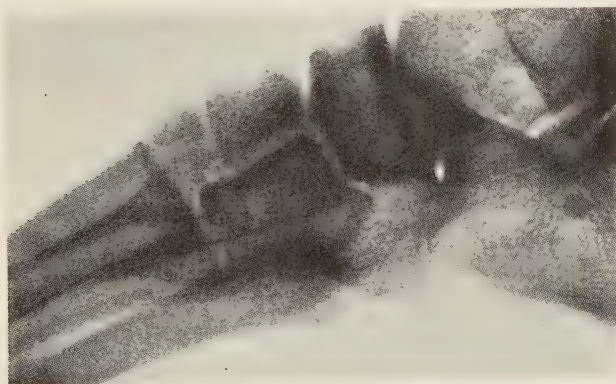


Fig. 7. (After *Barlow* 1942). See next Fig.



Figs. 7 and 8. (After Barlow 1942). Male, aged 82, bilateral finding. Verified by anatomical dissection.

References: *Barclay* 1932, *Barlow* 1942, *Bierman* 1922, *Boker & Müller* 1936—1937, *Flesch* 1877, 1879, *Friedlowsky* 1870, *Gruber* 1864, 1877, *Heidsieck* 1936, *Hohmann* 1934, *Holtby* 1916, *Neumann* 1939, *Pfitzner* 1896, *Stieda* 1869, *Volkov* 1902, 1904, *Watkins* 1937.

6. *Os cuneo-metatarsale I plantare* (*Pfitzner* 1896).
(= pars peronea metatarsale I)

The os cuneo-metatarsale I plantare is situated in close relationship to the proximo-fibulo-plantar corner of the first metatarsal. The bone is ab. the size of a cherry stone. It is not definitely visible in a radiograph, but may possibly be seen in a lateral oblique view.

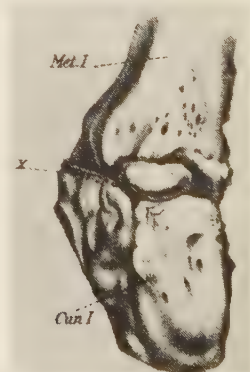


Fig. 9. (After *Pfitzner* 1896). Male, aged 64. Unilateral finding (no independent bone being present in the other foot, but only a similar formation indistinctly defined from the first metatarsal by a line of junction).

References: *Pfitzner* 1896.

7. *Os cuneo-metatarsale I tibiale.*

(= prehallux)

The os cuneo-metatarsale I tibiale is situated tibially, just off the joint of tibial cuneiform and first metatarsal. The bone is the size of a pepper-corn. Radiographically it is plainly visible from the dorsi-plantar aspect.

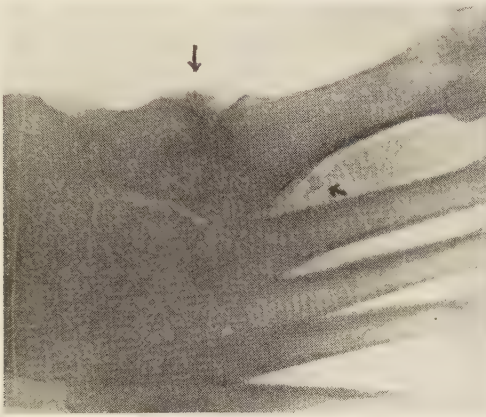


Fig. 10. Female, aged 67. Bilateral finding (in addition: arteriosclerotic a. dorsalis pedis) (BBH).

References: *Heimerzheim* 1925.

8. *Os cuneo-metatarsale II dorsale* (Güntz 1935).

The os cuneo-metatarsale II dorsale lies dorsally in the joint between the intermediate cuneiform and the second metatarsal.



Fig. 11. (After Güntz 1935). Male, aged 30, unilateral finding (right).

The bone, which is wedge-shaped with its base turning dorsally, is hardly pepper-corn-sized. It is difficult to discern in a radiograph, but may be seen in lateral or lateral oblique views.

References: *Güntz* 1935, *Schoen* 1935.

9. *Os in sinu tarsi* (*Gruber* 1888).

The os in sinu tarsi lies, as the name indicates, in the tarsal sinus. The bone is ab. the size of a big pea. It is difficult to see distinctly in a radiograph, but is said to be visible in a lateral view of the foot.

References: *Gruber* 1888, *Holle* 1938.

10. *Os intercuneiforme* (*Dwight* 1902).

The os intercuneiforme lies dorsally in the angle between the tibial and the intermediate cuneiforms and the navicular. The bone is hempseed-sized and is hardly visible in a radiograph.

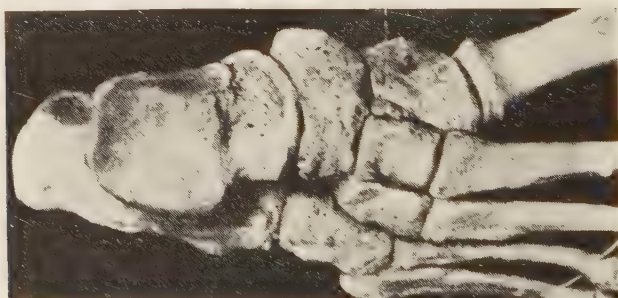
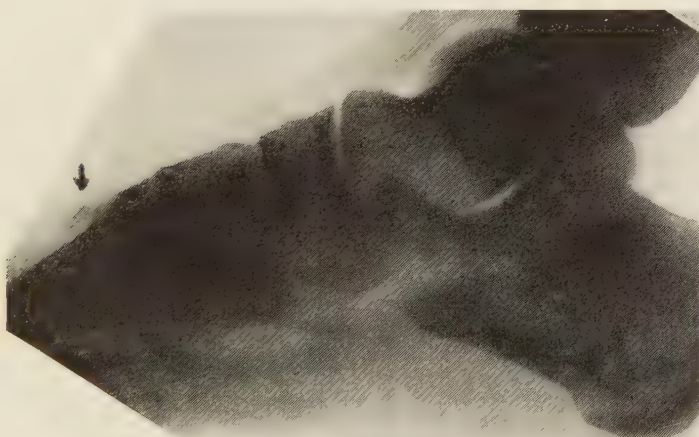
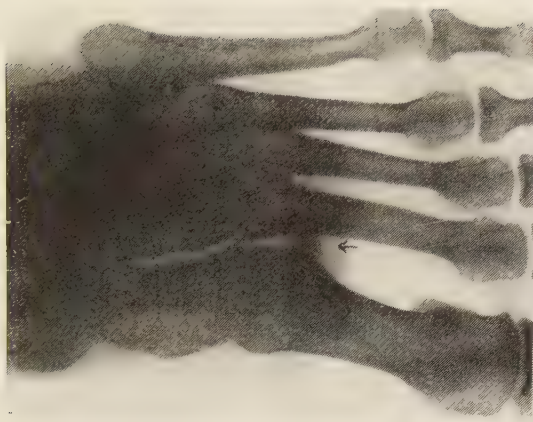


Fig. 12. (After *Dwight* 1902). Adult male, only right foot examined.

References: *Bierman* 1922, *Dwight* 1902, *Geist* 1914, *Holland* 1928, *Watkins* 1937.

11. *Os intermetatarsale I* (*Gruber* 1852).

The os intermetatarsale I, or intermetatarsium, is situated at the dorso-distal-fibular corner of the tibial cuneiform, between the first and the second metatarsal. The bone is generally spindle-shaped and may be up to 15 mm. long. It is best seen in a radiograph from the dorsi-plantar aspect.



Figs. 13 and 14. Female, aged 22, unilateral finding (BBH).

References: *Albrecht* 1886, *Arho* 1940, *Bibergeil* 1910, *Bierman* 1922, *Burman & Lapidus* 1931, *Bøcker* 1908, *Faber* 1934, *Francillon* 1934, *Friedl* 1924, *Gruber* 1852, 1877, 1878, *Hasselwander* 1910, *Heimerzheim* 1925, *Hohmann* 1934, *Holland* 1928, *Holle* 1938, *Köhler* 1924, 1939, *Loyer* 1920, *Lilienfeld* 1907, *Paal* 1933, *Pfitzner* 1896, *Schwalbe* 1917, *Tokmakoff* 1928—1929, *Volkov* 1902, *Watkins* 1937.

12. *Os intermetatarsale IV.*

The os intermetatarsale IV lies in the fourth intermetatarsal space. The bone is visible in a dorsi-plantar view of the foot.



Fig. 15. (After Köhler 1939).

References: Köhler 1939.

13. *Os interphalangeale.*

The os interphalangeale lies laterally in the interphalangeal joint. The bone is the size of the head of a good-sized pin. So far it seems to have been found only in the big toe. It is visible in a dorsi-plantar view of the foot.



Fig. 16. (After Hasselwander 1910). Male, aged 20. Only left foot examined. The os interphalangeale lies on the fibular side.

References: Hasselwander 1910.

14. *Os naviculare bipartitum.*

By the os naviculare bipartitum is understood a bipartition of the navicular, so that the shape and size of the normal navicular is obtained only by joining the two components together into a whole. Only cases of division in a tibial and a fibular segment seem to have been reported so far. This bipartition is easily recognizable in a dorsi-plantar view of the foot.



Figs. 17 and 18. (After Volk 1937). Male, aged 27,
unilateral finding (right).

References: Clausen 1944, Hohmann 1944, Licht 1941, Volk 1937, Zimmer 1938.

15. *Os naviculo-cuneiforme I dorsale* (Dwight 1902)

(= os paracuneiforme I = os infranaviculare).

The os naviculo-cuneiforme I dorsale is situated dorsally in the joint between the navicular and the tibial cuneiform. The



Fig. 19. Female, aged 57, unilateral finding (in addition there is found an os trigonum) (BBH).

bone is the size of a pepper-corn. It is best seen in a radiograph from the lateral or the lateral oblique aspect of the foot.

References: *Dwight 1902, Zimmer 1938.*

16. *Os paracuneiforme*
(= prehallux = precuneiform).

The os paracuneiforme is situated on the tibial side of the foot, in the plantar direction, and in close relationship to the joint between navicular and tibial cuneiform and/or proximal part of the tibial cuneiform. The bone may be the size of a hazel nut. Radiographically it is plainly visible in a dorsiplantar view of the foot.

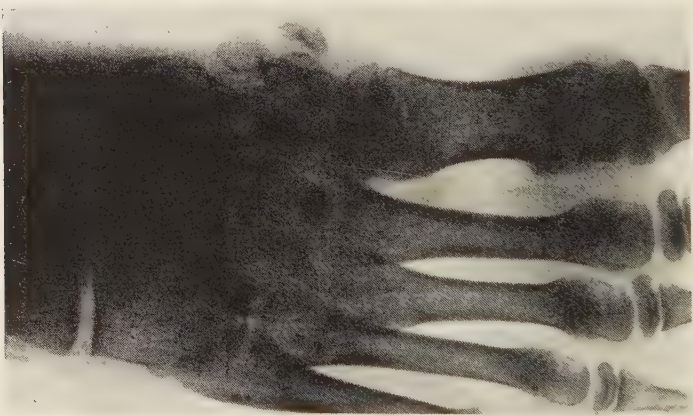


Fig. 20. Male, aged 13. Unilateral finding of ossa paracuneiformia.
(In addition unilateral os cuneiforme I bipartium) (OHK).



Fig. 21. (After *Burman & Lapidus 1931*). Bilateral finding from adult.
(Radiograph not fit for reproduction).

References: *Bardeleben 1889, 1894, Burman & Lapidus 1931, Cameron 1922—1923, Holland 1928, Tornier 1891, 1894.*

17. *Os peroneum* (Vesal 1555)

(= seamoid bone in the peroneus longus tendon
= cuboideum accessorius).

The os peroneum is situated on the fibular side of the cuboid in close relationship to the cuboid crest. The bone is rarely bigger than a coffee berry. Radiographically it is plainly visible from the dorsi-plantar, as well as the lateral and the lateral oblique aspects. The peroneum is not infrequently divided in two or three, even up to seven segments.

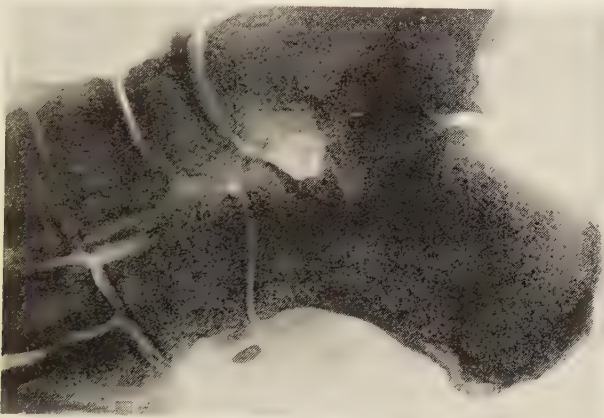


Fig. 22. Female, aged 48. Only left foot radiographed. (BBH).

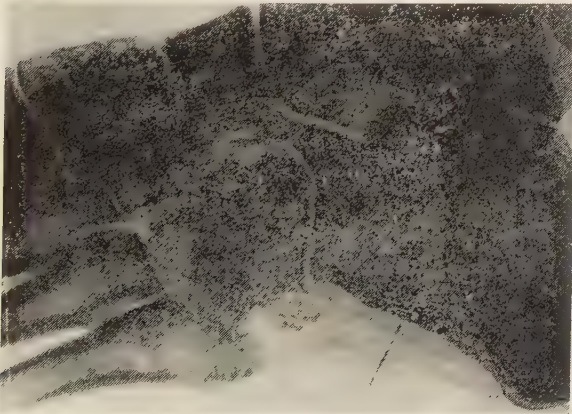


Fig. 23. Female, aged 49. Only right foot radiographed. (BBH).

References: *Arho* 1940, *Bibergeil* 1910, *Bierman* 1922, *Bizarro* 1920—1921, *Burman & Lapidus* 1931, *Bøcker* 1908, *Ehringer* 1909, *Fischer* 1912—1913, *Froelich* 1913, *Geist* 1914, *Gillette* 1872, *Grashey* 1912, 1939, *Güntz* 1942, *Haguier* 1937, *Heimerzheim* 1924, *Henderson* 1937, *Hohmann* 1934, *Holland* 1920—1921, 1928, *Holle* 1938, *Kohler* 1924, 1939, *Laquerrière* 1933, *Leimbach* 1938, *Lilienfeld* 1907, *Loyer* 1920, *Lunghetti* 1909, *Mouchet & Moutier* 1925, *Paal* 1933, *Pfitzner* 1892, 1896, *Retterer & Lelièvre* 1911, *Stieda* 1889, *Tornier* 1894, *Watkins* 1937.

18. *Os retinaculi* (Gruber 1863).

The os retinaculi is situated over the area of the bursa of the fibular malleolus, in such a manner that the superior peroneal retinaculum exits from the border turning back and downwards. The bone is flat, ab. $15 \times 10 \times 5$ mm., and radiographically it is visible in an antero-posterior view of the ankle joint.



Fig. 24. (After *Gruber* 1863). Old male, Unilateral finding. 1 = tibia, 2 = fibula, a = fibular anterior part of fibular malleolus, b = sulcus peroneorum, α = lig. mall. fib. ant. β = lig. mall. fib., post., 3 = os retinaculi (artificially displaced, backwards), γ = accessory ligament in joint between malleolus and bone.



Fig. 25. (After *Michelson* 1930). Male, aged 26.
Only left foot radiographed.

References: *Gruber* 1863, *Michelson* 1930.

19, 20, and 21. *Os sesamoideum interphalangeale* and *metatarsophalangeale*, and *os sesamoideum partitum*.

The interphalangeal sesamoid bones are situated on the plantar side in close relationship to the interphalangeal joints; rarely on the dorsal side. They are generally mesial and not bigger than rice.

The metatarsophalangeal sesamoid bones are situated on the plantar side close to the second, third, fourth, and fifth metatarsophalangeal joints as tibial and fibular sesamoid bones (in other words, corresponding exactly to the two constant sesamoid bones of the big toe). They are hardly bigger than pepper-corn. In rare cases there has been observed a mesial sesamoid bone in the big toe.

Metatarsophalangeal sesamoid bones situated on the dorsal side have been reported in a few cases.



Fig. 26. Female, aged 58. Sesamoid bones are seen corresponding to all metatarsophalangeal joints. As regards the second, third, and fourth, the tibial bones are even divided. In addition an interphalangeal sesamoid bone is seen in the big toe. (The left foot presented the same sesamoid bones, only none were divided). (BBH).



Fig. 27. Female, aged 55. Bilateral bipartition of the constant tibial sesamoid bone of the big toe. Unilateral bipartition of the interphalangeal sesamoid bone of the big toe. (BBH).

All the above sesamoid bones may be found divided. This is particularly the case with the two constant bones of the big toe, notably the tibial. The division consists most often in a fairly transverse bipartition. Yet, the line of cleavage may run any course, and the number of segments may vary almost indefinitely.

Radiographically these sesamoid bones are best seen from the dorsi-plantar aspect of the foot; in the cases of the metatarsophalangeal bones also on tangential pictures.

References: *Arho* 1940, *Bennet* 1935, *Bizarro* 1920—1921, 1921, *Boeminghaus* 1936, *Burman & Lapidus* 1931, *Bocker* 1908, *Fischer* 1912—1913, *Geist* 1914, *Gillette* 1872, *Goebels* 1935, *Grashey* 1912, 1939, *Hasselwander* 1910, 1938, *Henderson* 1937, *Hohmann* 1934, *Holland* 1920—1921, 1928, *Holle* 1938, *Igelstein* 1908, *Inge & Ferguson* 1933, *Kassatkin* 1934, *Kewenter* 1936, *Kimmerstiel*, *Kremser & Richter* 1933, *Koch* 1924, *Köhler* 1924, 1939, *Malgaigne* 1838, *Mayr* 1935, *Meis* 1928, *Momburg* 1907, *Müller* 1921, 1924, 1925, 1927, *Nesbitt* 1736, *Pfitzner* 1892, *Renander* 1924, *Retterer* 1884, *Schunke* 1901, *Stumme* 1908—1909, *Thilenius* 1895, 1896, *Watkins* 1937, *Weidenreich* 1922, *Wisbrun* 1934, *Wolf* 1912.

22. *Os subfibulare.*

The os subfibulare is situated just distal to the tip of the fibular malleolus. The bone may attain the size of a hazel nut. Radiographically it is plainly visible in an antero-posterior view of the ankle joint; but one may also succeed in seeing it in a dorsi-plantar view of the foot, with considerable plantar flexion of the foot.



Fig. 28. Female, aged 21, unilateral finding. (In addition fracture of fibular malleolus). (BBH).



Fig. 29. See next Fig.



Figs. 29 and 30. Male, aged 35, unilateral finding (BBH).

References: *Güntz* 1942, *Leimbach* 1938, *Schulte-Tenckhoff* 1929, *Trolle* 1945, *Watkins* 1937.

**23. *Os subtibiale* (*Bircher* 1918—1919)
(= *talus accessorius*).**

The *os subtibiale* is situated just distal to the tip of the tibial malleolus. The bone is hardly bigger than a hazel nut. Radiographically it is best seen in an antero-posterior view of the ankle joint, but it may also be seen in a dorsi-plantar view of the foot with considerable plantar flexion.



Fig. 31. Male, aged 47, bilateral finding. (BBH).

References: *Arho* 1940, *Bircher* 1918—1919, *Burman & Lapidus* 1931, *Grasmann* 1932, *Güntz* 1942, *Hohmann* 1934, *Holland* 1928, *Holle* 1938, *Lapidus* 1933, *Leimbach* 1938, *Puhl & Lindemann* 1938, *Trolle* 1945, *Volkman* 1933, *Watkins* 1937.

24. *Os supertalare* (*Bierman* 1921)
(= *astragalus secundarius*).

The *os supertalare* is situated on the dorsal side of the talus between the talocrural and the talonavicular articulations. The bone may reach the size of a pea. Radiographically it is plainly visible from the lateral or lateral oblique aspect of the foot.

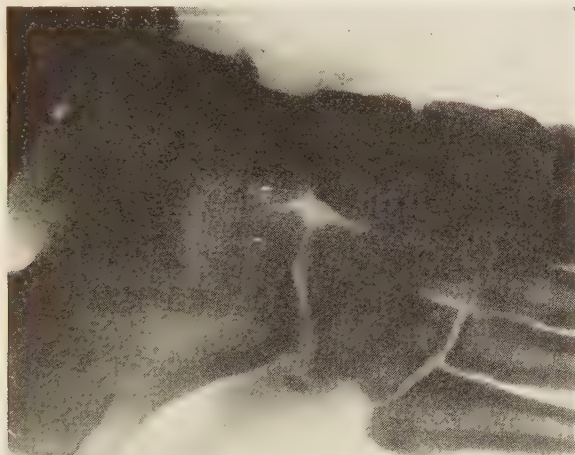


Fig. 32. Female, aged 27, bilateral finding. (In addition an *os peroneum*) (BBH).



Fig. 33. Female, aged 25, unilateral finding. (BBH).

References: *Bierman* 1921, 1922, *Burman & Lapidus* 1931, *Glogau* (after *Köhler* 1924), *Ribet & Cheveaux* 1928.

25. *Os sustentaculi proprium* (Pfitzner 1896).

The os sustentaculi proprium is situated just off the upper posterior corner of the sustentaculum tali calcanei. It may probably attain the size of a coffee berry. It is difficult to find on a radiograph, but one may succeed in an antero-posterior view of the ankle joint, where the foot is rotated outwards or has a maximal dorsal flexion.



Fig. 34. (After *Güntz* 1934). Male, aged 22, unilateral finding.

References: *Baer* 1904—1905, *Bierman* 1922, *Güntz* 1934, *Haselwander* 1910, *Hohmann* 1934, *Holland* 1928, *Holle* 1938, *Pfitzner* 1896.

26. *Os talo-calcaneare posterior*.

The os talo-calcaneare posterior lies in the posterior joint between the talus and the calcaneum. The bone may be up to bean-sized. Radiographically it is best seen from the oblique aspect indicated by *Anthonsen* 1943 for examination of the subtalar joint¹⁾.

¹⁾ The foot is placed in dorsally flexed position with the fibular side in touch with the film. The central ray is directed towards a point just under and behind the tip of the tibial malleolus, angled 25° cranio-distally and 30° dorso-ventrally. The focus distance is reduced to 25–35 cm.



Fig. 35. Male, aged 42. Only right foot radiographed. The bone has been verified at operation. (In addition there is found an os trigonum). (OHK).

References: Schnarberth 1939.

27. *Os talo-naviculare dorsale* (Pfitzner 1896)
(= os supranaviculare).

The os talo-naviculare dorsale lies dorsally in the joint between the talus and the navicular. The bone is generally

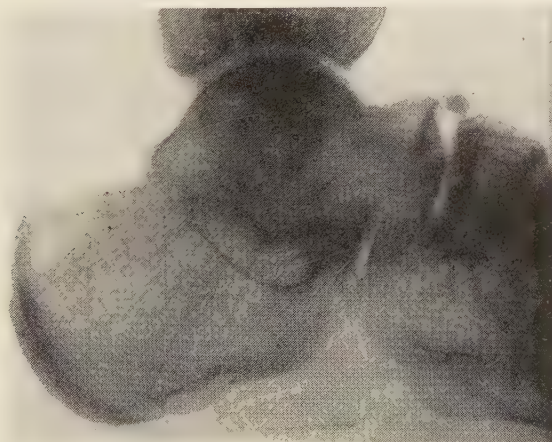


Fig. 36. Female, aged 21. Only right foot radiographed. (BBH).

smaller than a pea. Radiographically it is plainly visible from the lateral oblique aspect of the foot. Only rarely is it possible to see the bone from the dorsi-plantar aspect.

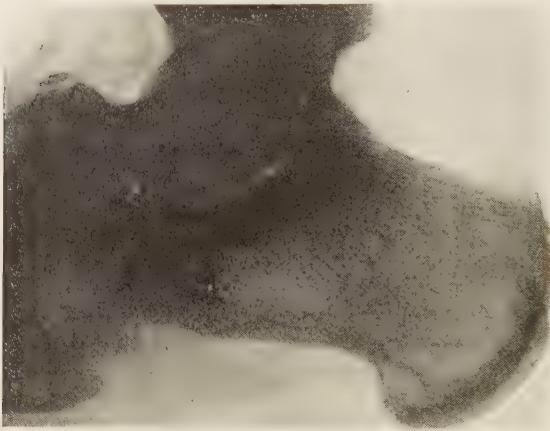


Fig. 37. Female, aged 37, bilateral finding. (BBH).

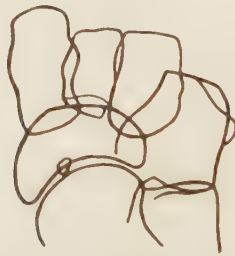


Fig. 38. Diagram of radiograph. Male, aged 44. (Only right foot radiographed). (BBH).

References: *Arho* 1940, *Bamatter* 1927, *Bierman* 1922, *Bizarro* 1920—1921, *Burman & Lapidus* 1931, *Esau* 1930, *Güntz* 1942, *Gocke* 1931, *Hasselwander* 1910, *Heimerzheim* 1925, *Hohmann* 1934, 1944, *Holland* 1920—1921, 1928, *Holle* 1938, *Köhler* 1924, 1939, *Leimbach* 1938, *Paal* 1933, *Pfitzner* 1896, *Pirie* 1920, *Reisner* 1930, *Schoen* 1935, *Schroder* 1931, 1937, *Sprengell* 1931, *Zimmer* 1938.

28. *Os talo-tibiale dorsale.*

The os talo-tibiale dorsale is situated just off the talocrural articulation on the extensor side of the joint. The bone may attain the size of a date. Radiographically it is visible in lateral oblique views of the foot.



Fig. 39. Male, aged 27. Only left foot radiographed. (In addition an os trigonum is seen). (OHK).

References: *Puhl & Lindemann* 1938, *Schossere* 1928.

29. *Os tendinis Achillis.*

The os tendinis Achillis lies in the Achilles tendon, in greater or smaller proximity to its point of attachment to the calcaneum. The bone varies greatly in size. Radiographically it can be



Fig. 40. See next Fig.



Figs. 40 and 41. Male, aged 64, unilateral finding. (BBH).

seen in a lateral view of the ankle joint. More than one bone is often seen in the same tendon.

References: *Güntz* 1942, *Haglund* 1928, *Hohmann* 1934, *Paal* 1933, *Schinz*, *Baensch & Friedl* 1939.

30. *Os tibiale* (*Bauhin* 1605)

(= *os tibiale externum* = *os naviculare accessorium* = *os naviculare secundarium* = *prehallux* = the sesamoid bone in the tendon of the *tibialis posterior*)¹).

The *os tibiale* is situated close to the proximo-plantar portion of the navicular tuberosity. The bone is probably rarely bigger

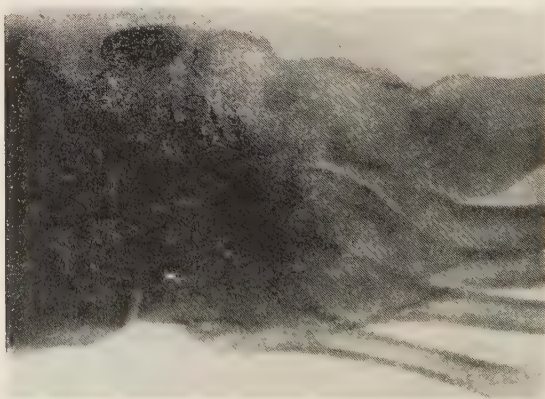


Fig. 42. Female, aged 23, bilateral finding. (BBH).

¹) Why the term *os tibiale* has been chosen appears from p. 165.

than a hazel nut. Radiographically it is best seen in a dorsi-plantar view of the foot, although it is not always possible to project it quite free of the navicular. It may, however, also be seen from the lateral or lateral oblique aspects. Occasionally one finds two, three, or more small bones together.

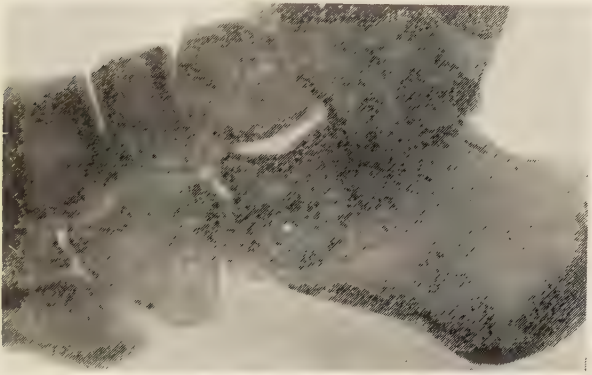


Fig. 43. Female, aged 41, bilateral finding. (BBH).



Fig. 44. Female, aged 32, Bipartite os tibiale. Only right foot radiographed. (BBH).



Fig. 45. Female, aged 32. Tripartite os tibiale. Bilateral finding (BBH).

References: *Anspach & Wright* 1937, *Arho* 1940, *Bardeleben* 1885, *Baur* 1885, *Bibergeil* 1910, *Bierman* 1922, *Bizarro* 1920—1921, *Blecher* 1908, *Burman & Lapidus* 1931, *Bocker* 1908, *Cameron* 1922—1923, *Cravener & Mac'Elroy* 1940, *Daniilides* 1929, *Ehringer* 1909, *Faber* 1937, *Fischer* 1912—1913, *Francillon* 1932, 1933, 1934, *Froelich* 1913, *Geist* 1914, *Gillette* 1872, *Grashey* 1912, 1939, *Gruber* 1871, 1877, *Güntz* 1934, 1942, *Haglund* 1906, *Hasselwander* 1903, 1910, *Henderson* 1937, *Henke*, *Barthel & Woytek* 1932, *Hensel* 1939, *Hohmann* 1934, 1944, *Holland* 1920—1921, 1928, *Holle* 1938, *Jensen* 1935, *Joltrain & Gally* 1929, *Kidner* 1929, *Kienbock & Müller* 1937, *Kohler* 1924, 1939, *Latten* 1927, *Laquerrière* 1933, *Leimbach* 1938, *Lilienfeld* 1907, *Loyer* 1920, *Lunggetti* 1909, *Luschka* 1858, *Manners-Smith* 1907, *Monahan* 1920, *Mouchet & Moutier* 1925, *Paal* 1933, *Pfitzner* 1892, 1896, *Saupe* 1939, *Thews* 1939, *Tornier* 1891, 1894, *Uhrmacher* 1934, *Volkov* 1902, 1904, *Waldeyer* 1904, *Watkins* 1937, *Weidenreich* 1923, *Zadek* 1926, *Zimmer* 1938.

31. *Os trigonum* (Rosenmüller 1804)

(= talus secundarius + talus accessorius = intermedium tarsi).

The os trigonum is situated immediately posterior to the talus close to the fibular tubercle of the posterior process of the talus and just above the calcaneum. The bone is hardly bigger than a hazel nut. Radiographically it is plainly visible both in lateral and in lateral oblique views of the ankle joint. There are found a few descriptions of bipartition of the trigonum.



Fig. 46. Female, aged 24, bilateral finding. (BBH).



Fig. 47. Female, aged 48. Only right foot radiographed.
(In addition a compact island in the calcaneum). (BBH).



Fig. 48. Female, aged 23. Only right foot radiographed. (BBH).

References: *Albrecht* 1883, 1886, *Arho* 1940, *Baastrup* 1923, *Bardeleben* 1883, 1884, *Baur* 1885, 1886, *Bennet* 1887, *Bibergeil* 1910, *Bierman* 1922, *Bizarro* 1920—1921, *Burman & Lapidus* 1931, *Bocker* 1908, *Ehringer* 1909, *Fischer* 1912—1913, *Francillon* 1934, *Friedlowsky* 1870, *Froelich* 1913, *Geist* 1914, *Grashey* 1912, *Gruber* 1864, *Güntz* 1942, *Hasselwander* 1903, 1910, 1914, 1921, *Heimerzheim* 1925, *Henderson* 1937, *Hohmann* 1934, *Holland* 1920—1921, 1928, *Holle* 1938, *Laquerrière* 1933, *Leimbach* 1938, *Lilienfeld* 1906, 1907, *Loyer* 1920, *Mouchet & Moutier* 1925, *Paal* 1933, *Pfitzner* 1896, *Shepherd* 1883, 1887, *Sochor* 1909, *Stieda* 1869, 1889, *Sutton* 1887, *Tornier* 1894, *Turner* 1883, 1887, *Volkov* 1902, *Watkins* 1937.

32. *Os trochleae*.

The os trochleae is a bone developed in the navicular fibro-cartilage. The bone is flat, 4 to 5 mm. in size, and is hardly recognizable in a radiograph. Its existence is not quite certain, however.

References: *Gillette* 1872, *Pfitzner* 1896, *Poirier, Charpy & Nicolas* 1926.

33. *Os tuberis calcanei* (*Heimerzheim* 1924).

The os tuberis calcanei is situated just off the calcanean apophysis. The bone may attain the size of 10 mm. Radiographically it is visible in lateral or lateral oblique views of the foot.



Fig. 49. (After *Heimerzheim* 1924). Diagram of radiograph of male, aged 30. Only one foot radiographed.

References: *Heimerzheim* 1924.

34. *Os unci* (*Pfitzner* 1896).

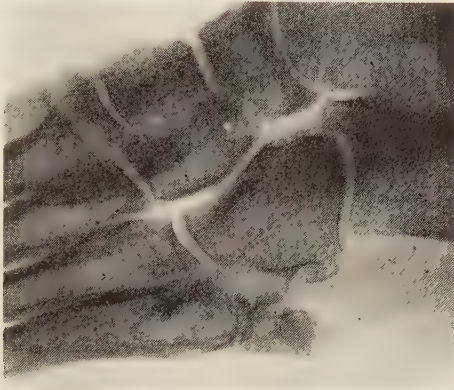
The os unci is situated immediately plantar to the fibular cuneiform. The bone is the size of a bean. Radiographically

it may, perhaps, be visible in a dorsi-plantar view of the foot, but its presence can never be ascertained with absolute certainty.

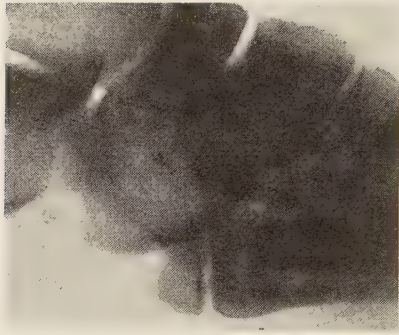
References: *Bierman* 1922, *Holland* 1928, *Lilienfeld* 1907, *Loyer* 1920, *Pfitzner* 1896.

35. *Os Vesalianum* (*Vesal* 1555).

The os Vesalianum is situated close to the proximo-fibular portion of the fifth metatarsal. The bone may attain the size of a shell-almond. It is visible in radiographs, both in dorsi-plantar and in lateral oblique views.



*Figs. 50 and 51. Female, aged 20, with closed epiphyses.
Unilateral os Vesalianum (FI).*



Figs. 52, 53, and 54. Male, aged 49. Unilateral os Vesalianum. Fig. 54 shows the other foot with no os Vesalianum. (OHK).



Fig. 55. Female, aged 77, with unilateral os Vesalianum. (An os peroneum is seen as well in a lateral view). (BBH).

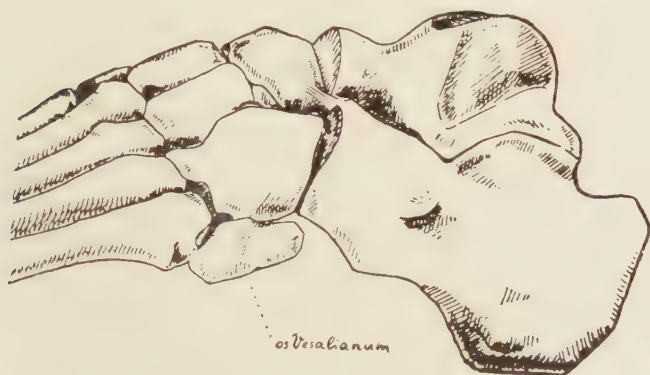


Fig. 56. (After Pilmanis 1933). An anatomical dissection preparation of a left foot with a completely independent os Vesalianum (nothing is stated of the other foot, nor of the patient's age and sex).

References: *Baastrop* 1921, *Bibergeil* 1910, *Bierman* 1922, *Burman & Lapidus* 1931, *Fischer* 1912—1913, *Froelich* 1913, *Gelinsky* 1904—1905, *Gruber* 1875, 1885, *Hasselwander* 1910, *Heimerzheim* 1925, *Hohmann* 1934, *Holland* 1920—1921, 1928, *Holle* 1938, *Johansson* 1922, *Kirchner* 1907, *Laquerrière* 1933, *Lilienfeld* 1906, 1907, *Loyer* 1920, *Mouchet & Moutier* 1925, *Pilmanis* 1933, *Spronck* 1887, *Watkins* 1937.

There is reason again to emphasize that this review of the accessory bones does not claim to be complete. I have included only the most common and those of the rarer ones which I have found partly in the literature and partly by personal examination. But, as will be shown in the following, there seems to exist an enormous variety of accessory bones.

Chapter 2.

OWN HISTO-EMBRYOLOGICAL INVESTIGATION OF HUMAN MATERIAL

It is a well-known fact that many incomprehensible morphological conditions in the adult individual may be accounted for through a study of the ontogenesis, which in many cases passes through all the stages of the phylogenesis. "The ontogenesis is a recapitulation of the phylogenesis" (*Haeckel's* law). This recapitulation (by *Haeckel* called *palingenesis* and by *Sewertzoff* *phylembryogenesis*) applies among others to the skeleton of the foot (*Sewertzoff* 1931).

A histo-embryological investigation of the feet must, therefore, be expected to be able to give information on a possible phylogenetic origin of the accessory bones present in the foot. Such an investigation constitutes the main issue of my work. An investigation of this kind must be planned on a large scale to be of any value. This means that one must make histo-embryological examinations of successive serial sections of numerous human embryonic feet at different ages. Many difficulties will naturally arise in connection with the carrying out of a work of this scope:

1. A large material is necessary, because many of the accessory bones are rare. The larger the material the better.
2. It is difficult to obtain a sufficiently fresh material of the smallest embryos, particularly those where the primordia are still at the prochondral stage. (Such were almost impossible for me to procure, because most of the embryos of this age were rotten).
3. It is absolutely necessary to make systematic successive serial sections with examination of each individual section.

Very often it happens that one believes to have found an accessory bone, only to discover, after examination of about a dozen sections, that the supposed bone is no more than a projecting osseous process separated in the first sections from the bone to which it is attached.

4. The systematic serial-section examinations make such an investigation an exceedingly long and troublesome task. The technical and manual parts require long time and the histological examinations much work.

5 Last, but not least, an investigation of this kind is a very expensive affair, because it requires large numbers of cover slips and slides. Moreover, the manual part of the work cannot be made without aid, if the investigation is to be carried through within a reasonable space of time.

I. AGE ESTIMATION OF EMBRYOS.

My embryological material comprises 508 feet of different ages, ranging from 6 to 27 weeks (menstruation age). Each embryo is measured from crown to rump (if it was a whole embryo) with an accuracy of one millimetre, and each foot from heel to longest toe with an accuracy of one-tenth millimetre. (In the few cases where there was a slight difference in length between the two feet the mean value was noted down).

The ages are calculated from the graph indicated below, which I have constructed on the basis of *Keibel & Mall's* 1910, *Mall's* 1918, *Streeter's* 1921, and *Scammon's* 1937 tables. These curves have been controlled in a previous paper (1947).

The weights were not considered in my material, partly because the embryos were not equally fresh, and partly because, according to *Siebert* 1941, the weights are subject to greater individual variations than the lengths.

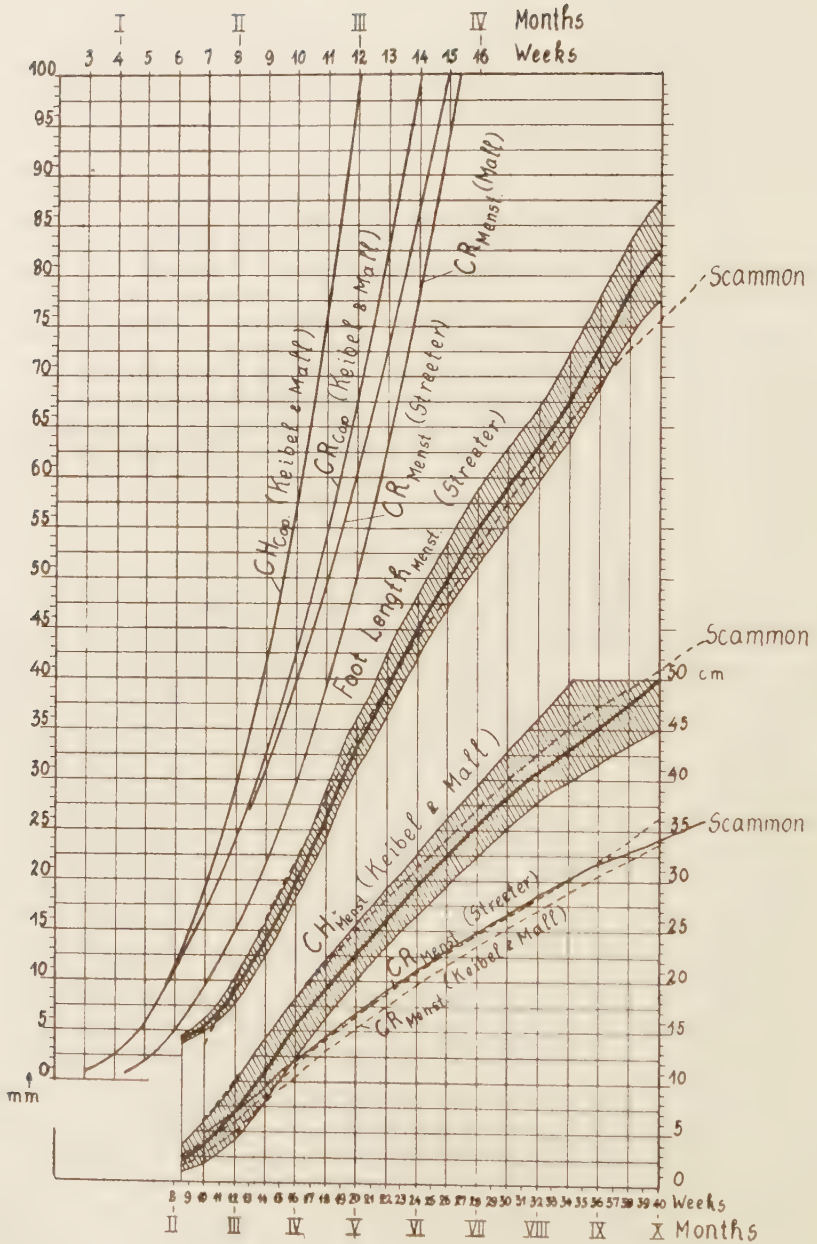


Fig. 57. A graph constructed on the basis of Keibel & Mall's 1910, Mall's 1918, Streeter's 1921, and Scammon's 1937 tables. The age of a human embryo can be estimated by means of this graph, if one knows the crown-heel length (CH), the crown-rump length (CR), or the foot length. In addition to the mean values also the extreme values (the hatched areas)

II. TECHNICAL TREATMENT OF EMBRYONIC FEET

The 508 feet were made up of pairs in order thus to be able to procure information on possible bilateralism of the accessory bones. When only pairs of feet are examined the objection might be raised, where accessory bones occurring bilaterally are concerned, that actually the material comprises only half the indicated number, in the present case 254.

The material was treated in the following manner:

The embryos were derived from women admitted to different Copenhagen hospitals for abortion (spontaneous as well as criminal). Only a small number had been admitted for induced abortion. Immediately after expulsion the embryos were as quickly as possible placed by the nurses in an aqueous formalin solution.

After having been collected each embryo was numbered and measured (crown-rump length (CR), foot-length, and possibly crown-heel length (CH)), and its sex was estimated (if the CR exceeded 90 mm.).

Next the feet were cut off proximal to the ankle joint and placed in formol-sublimate-glacial acetic acid. After washing, increasing concentrations of alcohol, alcohol iodine, nitric acid, and alum water; washing, and again increasing concentrations of alcohol; embedding in paraffin.

The cutting was a systematic serial-section cutting, where the individual sections were 10 μ thick in the great majority of the cases and 15, 20, or 25 μ thick in a small number. All the sections were mounted on slides in exact consecutive order. The sections of all the right feet were cut so as to run parallel with the foot sole, while those of the left feet were frontal sections cut at right angles to the foot sole.

Staining with Hansen's haematoxylin and orange.

Histological examination with a routine magnification to 60 times the normal.

were indicated by *Keibel & Mall* for the CH and by *Streeter* for the foot length. The added: cop. and menst. mean that the age is calculated from the copulation and the first day of the last menstruation respectively. The curves of the various writers are not quite concordant. In a previous paper (1947) I have shown that the curves which accord best with facts are the following: *Streeter's* foot-length curve with borderline values, *Streeter's* CR-curve, and *Scammon's* CH-curve.

Deviations were made in certain cases from this standard procedure: a) in the cases of very small embryos whose feet were hardly more than plates, and b) in the cases of a number of bigger feet (25 to 55 mm. long).

ad a: The staining was here undertaken according to *Steiner* 1922, i. e. with haemalum, mucicarmine, and picric acid, in order to make the prochondral cartilage plainly visible in these small feet.

ad b: A number of bigger feet were embedded in celloidin. The procedure was at first that of the standard method, but after decalcification with nitric acid the feet were stained *in toto* with Hansen's haematoxylin in alum water to avoid subsequent staining of each individual section. The staining did not suffice, however, so after-staining of the sections (as indicated above) proved necessary.

The celloidin blocks were cut under running 70 % alcohol in systematic serial sections 50 μ thick. The sections were mounted by means of flame fixation. It was somewhat difficult to make the sections stick to the slides, but this difficulty was in a great measure overcome by the following procedure: The sections were placed direct from the 70 % alcohol on the slides, on which a mixture of albumen and glycerol had been rubbed. 5 or 6 layers of filter-paper steeped in 96 % alcohol were laid over each section, and on top of these another slide. The two slides were pressed against each other and passed three or four times through a flame.

Finally pieces of the left feet of 25 normal, full-term, but still-born children were taken out and examined. The pieces, taken from the area round the navicular tuberosity, were treated and cut in serial sections as indicated under b.

Well over 300,000 sections were cut and examined histologically, and well over 10,000 slides and corresponding cover slips were applied for these examinations.

III. THE 4-STAGE DEVELOPMENT OF THE BONES

Before passing on to a detailed description of own histological investigations there is reason just to outline the 4-stage ontogenetic development of the bones. The 4 stages are as follows: 1. *mesenchymal*, 2. *prochondral*, 3. *cartilage*, and 4. *bone*. This does not mean, however, that all the bone elements reach the same developmental stage within exactly the same period.

1. *The mesenchymal stage* manifests itself histologically by condensation of the mesenchymal tissue, because the mesenchymal cells proliferate and settle densely packed. The cell boundaries are difficult to distinguish. Simultaneously with the condensation there occurs a considerable vascularisation of the tissue. It is not yet possible to discern individual bone elements. The mesenchymal stage for bones presents no differences in density from the corresponding stages for muscles and tendons, for instance (*Petri* 1935).

2. *The prochondral stage* is defined differently by the different writers. Personally I adhere to *Steiner's* 1922 and *Petri's* 1935 definition of prochondral cartilage. According to these writers we speak of prochondral cartilage when the homogeneously dense mesenchyma is seen to contain isolated nests differing from the remaining tissue, at first by a concentric arrangement of the cells, and later by the presence of a matrix staining rose-red with mucicarmine. Histologically it appears that the cells in the nests increase in size with big and oval nuclei, and that the peripheral parts of the cells are converted into cartilaginous matrix.

3. *The cartilage stage* corresponds to the presence of hyaline cartilage. According to *Senior* 1929 the chondrofication of the elements of the foot sets in in the following order:

2nd, 3rd, and 4th metatarsals — cuboid — 5th metatarsal — calcaneum — talus — fibular cuneiform — intermediate cuneiform — tibial cuneiform — 1st metatarsal — navicular — proximal phalanges of 2nd, 3rd, and 4th toes — proximal phalanx of 5th toe — proximal phalanx of big toe — middle phalanges of 2nd, 3rd, and 4th toes — middle phalanx of 5th toe — terminal phalanx of big toe — terminal phalanges of 2nd, 3rd, and 4th toes — terminal phalanx of 5th toe.

4. *The bone stage* begins with the first traces of ossification.

There is some disagreement as to when the individual tarsal elements are first plainly distinguishable. Thus *Baur* 1886, *Strauss* 1927, *Hintsche* 1930, and *Schmidt-Ehrenberg* 1942 state that at a CR of 18 to 19, 14, 14, and 15 mm. respectively the individual elements cannot be differentiated, while *Leboucq* 1886 and *Hintsche* 1930 find that the individual elements are distinguishable at a CR of 12 and 15.8 mm. respectively.

Schomburg 1900 and *Bardeen* 1905 hold that the mesenchymal stage extends over the 4th and the 5th week, and that the pro-chondral stage commences after the 6th week.

With regard to the tarsal and metatarsal primordia my embryological investigations show the following embryonic ages for the different stages:

3 embryos (104, 129, and 188) with CRs ranging from 12 to 15 mm. prove to be at the mesenchymal stage. According to *Keipel & Mall's* CR-curve these embryos are from 6 to 6½ weeks old (copulation age). *Streeter's* curves, which I otherwise generally apply, do not comprise such small embryos.

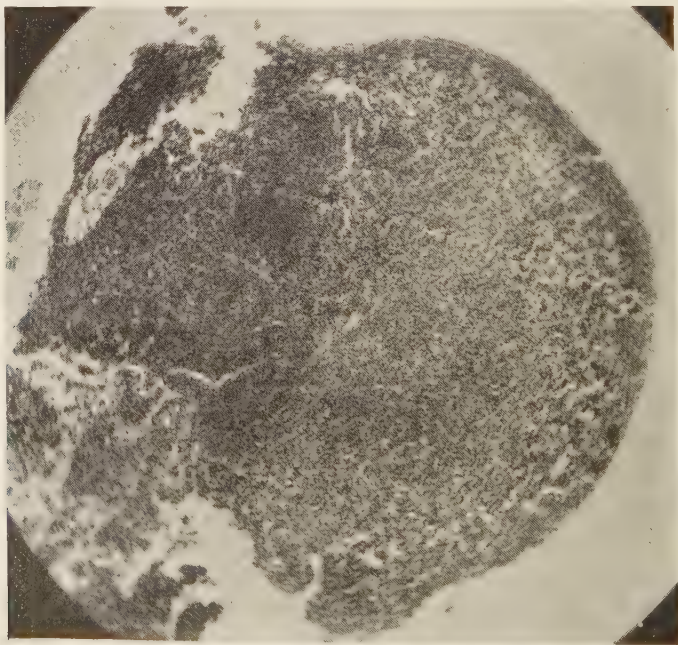


Fig. 58. 104 D. Mesenchymal stage, section 10 μ thick, magnified 85 times. The entire primordial extremity is seen as a plate. The future bones cannot yet be differentiated.

2 embryos (6 and 289) with CRs ranging from 15 to 20 mm. prove to have reached a transitional stage between mesenchyma and prochondral cartilage. A few elements are traceable, but nothing certain could be stated. According to *Keibel & Mall's* CR-curve these embryos are between $6\frac{1}{2}$ and $7\frac{1}{2}$ weeks old (copulation age). *Streeter's* curves cannot be used for these embryos either.



Fig. 59. 289 D. Prochondral stage, section $10\ \mu$ thick, magnified 43 times. Calcaneum, talus, and cuboid present prochondral centres. Remaining primordial tarsus allows of no differentiation. The 5 rays are plainly visible, a few primordial metatarsals are found to be at the point of transition to prochondral formation. Be it remarked that only the 4th ray is connected with the primordium of the cuboid, while the 5th ray is independent of it. (Tibia and fibula in cartilage).

3 embryos (130, 269, and 287) with CRs ranging from 20 to 25 mm. prove to have attained the stage of transition from prochondral cartilage to cartilage. The centres of the individual elements are here plainly discernible, but peripherally the elements are found to fuse with the surrounding tissue. In 130 a bilateral double centre is plainly visible in the tibial cuneiform. According to *Keibel & Mall's* CR-curve these em-

bryos are between $7\frac{1}{2}$ and 8 weeks old (copulation age). These embryos are likewise too small for *Streeter's* curves to be applicable.

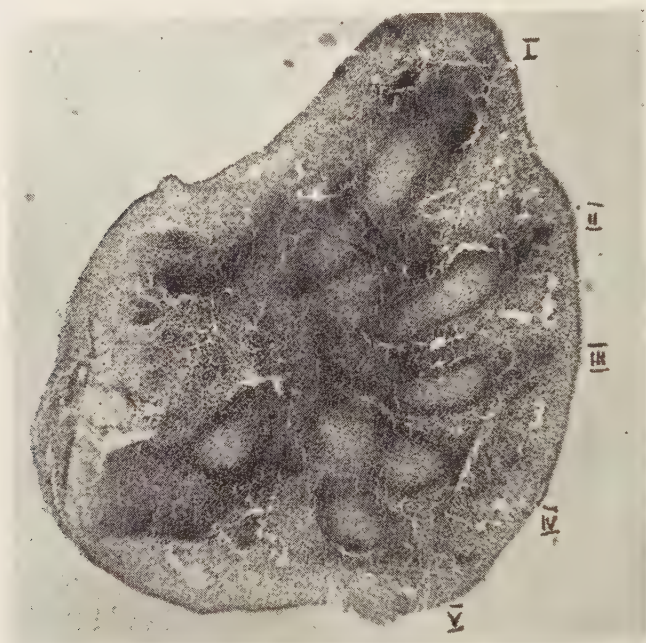


Fig. 60. 269 D. Prochondral stage with partial transition to cartilage stage. Section $10\ \mu$ thick, magnified 60 times. All the primordial metatarsals as well as the cuboid are plainly visible. The 3 primordial cuneiforms are distinguishable. Be it remarked that here, too, only the 4th ray is connected with the primordium of the cuboid. (Tibia and fibula in cartilage).

Except for the stated finding of a bipartite primordium of the tibial cuneiform I have found no divided primordial tarsal or metatarsal elements in these embryos. Neither have I found other accessory bone primordia. Indeed, there was found a markedly dense mesenchymal tract between the tip of the tibial malleolus and the navicular tuberosity. I dare not, however, attach any importance to this finding, partly because such tracts may be found also between other elements, e. g. between the calcaneum and the navicular, and partly because *Petri* 1935 has shown that the mesenchymal stage for bones does not differ from the corresponding stages for muscles, tendons, and ligaments.

All the embryos with a CR of 25 mm. or more have reached the cartilage stage (with regard to tarsal and metatarsal development). This means that all embryos which, according to *Keibel & Mall*, are 8 weeks old (copulation age) or more have reached the cartilage stage (*according to Streeter's CR-curve all embryos with a CR of 25 mm. or more are likewise over 8 weeks old (menstruation age)*). The future bone elements have not attained their final shapes within the first part of the cartilage stage. Thus, for instance, the future processes are at first seen only as prochondral outgrowths.

The primordial phalanges are laid down a little later than the primordial tarsals and metatarsals. The phalanges develop in the order of proximal, medial, and terminal phalanges. The tibial precede the fibular. The embryos are 9 to 10 weeks old (copulation age) = *9 to 11 weeks old (menstruation age)* before all the phalanges have reached the cartilage stage.

The constant sesamoid bones develop still later, i. e. not till the embryos are 10 to 11 weeks old (copulation age), = *11 to 12 weeks old (menstruation age)*. (A more detailed description is given p. 74).

It appears from what has been stated above that when the prochondral stage is attained one can begin to discern separate nests within the homogeneously dense mesenchyma. But nothing certain is known as to whether each of the future independent hyaline cartilage elements arises from a number of prochondral nests corresponding to the development of the element concerned from the primitive tetrapod foot elements, or whether the number of nests is independent thereof. (cf. *Ursing's* findings, 1932, concerning the calcaneum in *bradypus tridactylus* (edentata — mammals)). As, moreover, there are found no sharp lines of division between the individual prochondral nests or between groups of several prochondral nests, it seems to me justifiable to require that *only if an accessory bone has been demonstrated as an independent hyaline cartilage element can it be said for certain to have been laid down independently*. A primordium which has been demonstrated as an independent element only at the prochondral stage is not conclusive — as long as our knowledge is not greater. Hence my proper embryological material comprises exclusively embryos from the cartilage stage of development.

the deviations were generally within the range of one week (*vide* the author 1947). Where such deviations were present the age estimation was based on the foot length.

That there are found figures higher than 250 is not due to a selection of the material, but partly to the fact that I failed with the cutting of some of the feet, and particularly to the fact that the examined feet were chosen at random from among almost 400 embedded pairs of feet.

A. THE INDIVIDUAL ACCESSORY BONES PREFORMED IN HYALINE CARTILAGE AND THEIR PERCENTAGE FREQUENCIES

1. *Calcaneus accessorius*.

The calcaneus accessorius is found preformed in hyaline cartilage in 2 cases: 20 (17 to 18 weeks) and 66 (18 to 19 weeks). In 20 it is found in the right foot, and in 66 in both feet, but here the left cartilage centre is about 3 times as big as the right.

This gives the following percentage frequencies:

1 pair and 1 single among 250 pairs: $0.8\% \pm 0.6$.

3 feet among 500: $0.6\% \pm 0.5$.

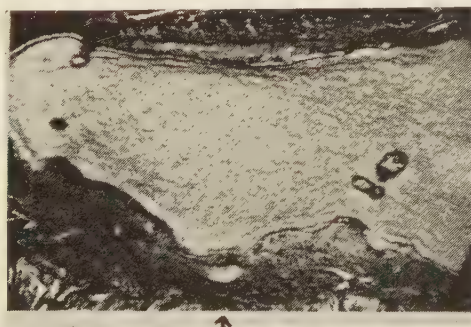


Fig. 61. 20 D (17 to 18 weeks). Section $30\ \mu$ thick, magnified 22 times. The calcaneum is seen with the independent calcaneus accessorius, which is found in 12 sections, of which this is the 6th.



Fig. 62. 66 S (18 to 19 weeks). Section 30 μ thick, magnified 22 times. The calcaneum is seen here together with a little bit of the talus in the upper right corner. The independent calcaneus accessorius is seen in 10 sections, inferiorly to the left of the calcaneum. This section is the 7th. Like in the preceding picture the calcaneus accessorius is seen to be situated in close relationship to the calcaneum imbedded in its pericondrium. The trochlear process of the calcaneum is observed just above the calcaneus accessorius, and above this again the tendons of the peroneal muscles (the short was during the cutting torn out of its sheath and led down to the long).

2. *Os cuneiforme I bipartitum*.

The os cuneiforme I bipartitum is found preformed in hyaline cartilage in the following pairs of feet:

	216			229 42		348		134	160
weeks	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17

The phenomenon proves to be bilateral in all cases, though occasionally with a slight difference between the two feet (what this means appears from the following).

This gives the following percentage frequencies:

6 pairs among 250 pairs: $2.4\% \pm 1.1$.

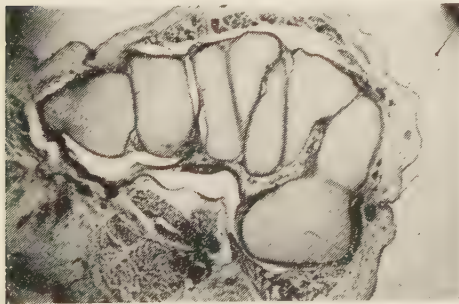
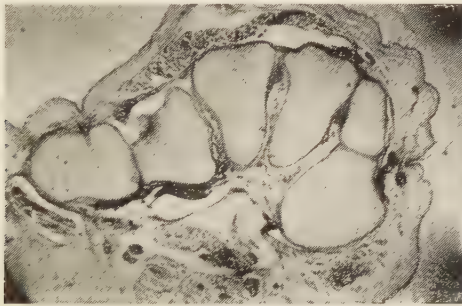
12 feet among 500: $2.4\% \pm 0.8$.

Only 216 presents 2 completely separated cartilaginous elements. In the other cases there is seen fibular union in the middle. These cases have nevertheless been included among those of bipartite tibial cuneiform, in conformity with *Pfitzner's* 1896 statement that there was found union in 3 of his 4 cases

of complete bipartition, in one of these even a slight synostosis (as will be mentioned later, coalescence may arise where there is found synchondrosis).



Fig. 63. 216 S (8 to 9 weeks). Section $10\ \mu$ thick, magnified 100 times. In this embryo there is seen complete bipartition of the tibial cuneiform. The section shows this beautifully. The centres of the tibial and fibular cuneiforms are visible to the left of the os cuneiforme I bipartitum.



Figs. 64 and 65. 348 S (13 to 14 weeks). Sections $10\ \mu$ thick, magnified 22 times. The former picture shows (to the right) complete separation between the plantar and the dorsal element. The latter picture illustrates what is understood by the fibular union in the middle. The coalescence is seen in 28 sections. This is the 14th, where the coalescence is at its highest. The tibial cuneiform is seen in 127 sections, 56 before the coalescence and 43 after.

On the other hand I am quite aware of the fact that the relatively high frequency of bipartite tibial cuneiform may be accounted for on the assumption that the primordial tibial cuneiform always is bipartite, but that the two element fuse in the great majority of cases. The fact that I found only 2 completely separated cartilaginous elements at the earliest stage seems to argue in favour of this hypothesis. (It is worth noting that I found a similar case: 130, also at the prochondral stage).

3. *Os intermetatarsale I.*

The os intermetatarsale I is found preformed in hyaline cartilage in the following pairs of feet:

				267	336	339	250		
			79	307	157	209	249		
			24	3	32	41	233		168
	350					25	163	330	234
weeks	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17

The element is by no means equally developed in both feet. There may be found a large intermetatarsium in one foot and only a small one in the other, or a well-developed intermetatarsium in one foot and not be slightest trace of one in the other.

An intermetatarsium is found 14 times bilaterally and 6 times unilaterally (4 right feet and 2 left), which means that it is bilateral in 70 per cent.

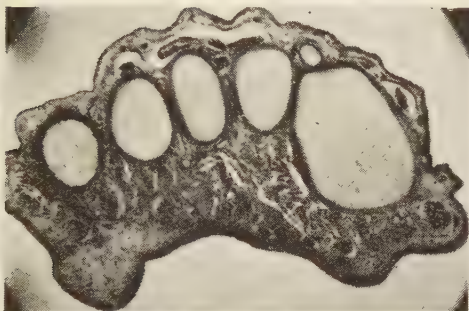
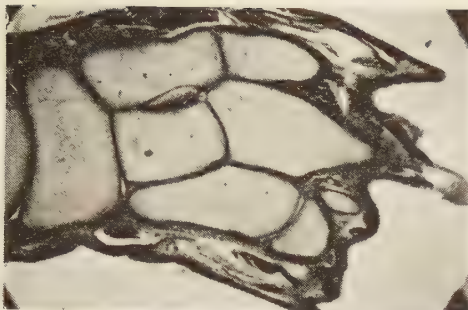
This gives the following percentage frequencies:

14 pairs and 6 single among 250 pairs: $8.0\% \pm 1.7$.

34 feet among 500: $6.8\% \pm 1.1$.

Synchondrosis is found in 2 cases: 233 D (thus unilaterally), where there is partial synchondrosis to the disto-tibio-dorsal corner of the intermediate cuneiform, and in 267 (bilaterally), where there is almost complete synchondrosis to the disto-fibulo-dorsal corner of the tibial cuneiform.

A large well-developed intermetatarsium (as that shown in Figs. 55 and 67) is 210μ thick and 555μ long. This corresponds in the present case to one-third of the length of the 1st metatarsal, but in most cases the length of the intermetatarsium is only from one-fourth to one-fifth of that of the 1st metatarsal.



Figs. 66 and 67. 25 D and 25 S (13 to 14 weeks). Sections $15\ \mu$ thick, magnified 22 times. In Fig. 66 the navicular is seen to the left, after which follow the 3 cuneiforms, which are connected with the bases of the 3 tibial metatarsals. The spindle-shaped intermetatarsium is seen between the 1st and 2nd metatarsals. Fig. 67 shows the 5 metatarsals with the intermetatarsium lying dorsally between the 1st and the 2nd metatarsal.

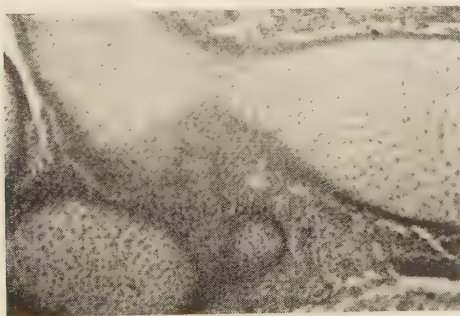


Fig. 68. 350 D (8 to 9 weeks). Section $10\ \mu$ thick, magnified 100 times. The 2nd metatarsal is seen superiorly extending over the entire length of the picture. The base of the 1st metatarsal is seen in the lower left corner, and just in front of this the intermetatarsium. It was present in 5 sections. This is the 3rd.

4. *Os interphalangeale*.

The os interphalangeale was found preformed in hyaline cartilage in the following pairs of feet:

	53	214	355		
			257		20
weeks	13-14	14-15	15-16	16-17	17-18

This bone is in all 5 pairs of feet found laterally and on the plantar side in the joint between the proximal and terminal phalanges of the big toe. In 4 of the pairs there are found interphalangeal sesamoid bones as well in the same joint, whereas such are not found in the 5th pair (355).

The primordial os interphalangeale is found both tibially and fibularly, and bilaterally as well as unilaterally (20 D & S tibially; 53 D, 214 S, and 257 D fibularly; and 355 D & S tibially).

A calculation of the frequency of the os interphalangeale shall most reasonably be based only on embryos over 12 weeks old, for — as shown p. 74 — the 2 constant sesamoid bones are not definitely preformed till this age. 187 of the embryos are over 12 weeks old.

The percentage frequencies are therefore:

2 pairs and 3 single among 187 pairs: $2.7\% \pm 1.2$.

7 feet among 374: $1.9\% \pm 0.7$.

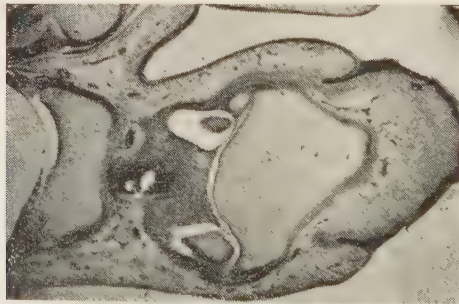


Fig. 69. 257 D. (15 to 16 weeks). Section $15\ \mu$ thick, magnified 22 times. The base of the terminal phalanx of the big toe is seen in the centre of the picture. To the left of it we find, in order from above downwards: fibular os interphalangeale (found in 10 sections, this is the 4th), commencement of proximal phalanx, a beginning interphalangeal sesamoid bone, and again commencement of proximal phalanx.

In 2 of the unilateral cases (214 and 257) the interesting phenomenon is observed that in one foot there is found an independent cartilaginous primordium, while the other foot presents a similar formation, only the latter is continuous with the base of the terminal phalanx connected by a thin stalk. A similar spur-like formation may be formed also on the opposite side of the same phalanx (e. g. 214 D). Fig. 70 will illustrate the facts.



Fig. 70. 2 diagrams of the interphalangeal joint of the big toe, showing as follows from left to right: os interphalangeale, spur-like formation, the same, and interphalangeal synchondrosis brought about by spur.

The question naturally suggests itself whether the os interphalangeale is not simply such a spur which has been constricted off. This may be so, but the reverse may also be the case, since in some cases, e. g. 53 (13 to 14 weeks), there is found an independent primordial bone on the fibular side in the right foot, but no such bone nor spur in the left.

Interesting is also the fact that such a spur may cause synchondrosis between the phalanges. This I find to have happened with the phalanges of the big toe in 2 cases (will be described further under synchondrosis p. 100).

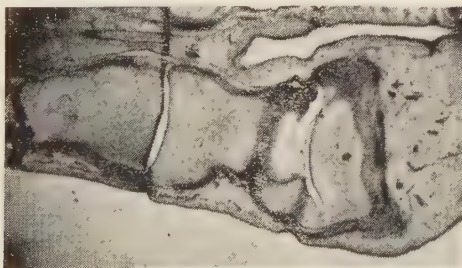


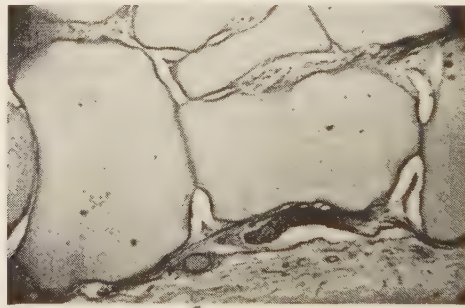
Fig. 71. 329 D (14 to 15 weeks). Section 10 μ thick, magnified 22 times. From left to right: head of 1st metatarsal, proximal phalanx, and base of terminal phalanx. On the tibial side of the latter (inferiorly in the picture) the spur connecting the proximal phalanx with the terminal is seen (the dark streak on the spur is due to a fold in the preparation).

5. *Os paracuneiforme*.

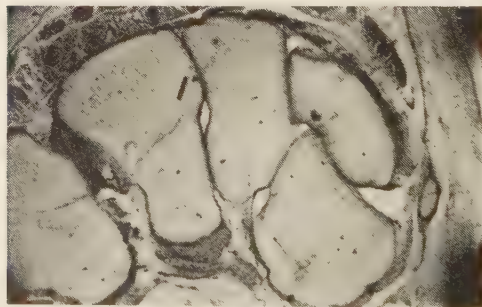
The *os paracuneiforme* is found preformed in hyaline cartilage in the following pairs of feet:

					330		347			
	324		305		264	252	263	147		
	284		217	318	257	143	192	174		
	229	302	194	265	202	84	136	63		197
	162	190	161	259	87	26	21	261		68
weeks	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	19-20	20-21

The *paracuneiform* is not always equally developed in both feet. Thus there may be found a big *paracuneiform* in one foot and a small one in the other. But the bone never occurred unilaterally in the present series. Most often, however, the cartilaginous elements were equal in size in both feet.



↑



←

Figs 72 and 73. 252 D and 252 S (16 to 17 weeks). Sections 10 μ thick, magnified 22 times. Fig. 72 shows, from left to right: tip of the head of the talus, navicular, tibial cuneiform, and finally the base of the 1st metatarsal is just visible. The *paracuneiform* is seen inferiorly, between the navicular and the tibial cuneiform. It is visible in 27 sections. This is the 19th. In Fig. 73 we find from left to right: cuboid, fibular, intermediate, and tibial cuneiforms (the latter superiorly), and under the tibial cuneiform the navicular. The *paracuneiform* is situated off the interval between the latter two. It is visible in 20 sections. This is the 13th.

The relative size of the paracuneiform is independent of the age of the embryo. This is a fact of great interest, because the paracuneiform is of frequent occurrence in embryos, whereas the bone is extremely rare in adults, in whom it has been observed only a few times.

The percentage frequencies of the paracuneiform in my embryological material are as follows:

33 pairs among 250 pairs: $13.2\% \pm 2.1$.

66 feet among 500: $13.2\% \pm 1.5$.

Finally it may be added that among 18 left feet from normal, full-term, but still-born, children 2 present a paracuneiform i. e. $11\% \pm 7.4$.

6. *Os peroneum*.

The os peroneum is found preformed in hyaline cartilage in 1 case: 140 (17 to 18 weeks). This peroneum is plainly visible in the right foot in 15 sections. Its relative size corresponds to that of the os peroneum known to occur in adults. In the left foot the peroneum is found to be smaller, and particularly it shall be pointed out that it is quite flat.

The os peroneum lies completely imbedded in the peroneus longus tendon.

Percentage frequency: $0.4\% \pm 0.4$.

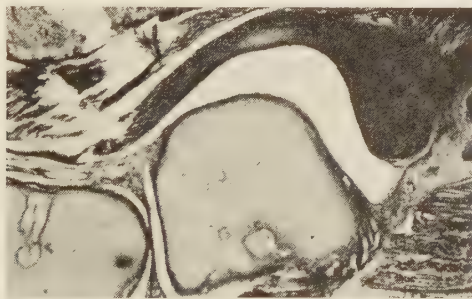


Fig. 74. 140 D (17 to 18 weeks). Section $10\ \mu$ thick, magnified 22 times. The cuboid is seen in the middle, and to the left of it we find the distal part of the calcaneum. Above the cuboid the peroneus longus tendon is seen creeping round the fibular edge of the cuboid and turning down towards the plantar surface of the foot. The peroneum, which is seen imbedded in the tendon, is visible in 15 sections. This is the 11th.

7. *Ossa sesamoidea*¹⁾.

The sesamoid bones¹⁾ reach the hyaline cartilage stage later than the constant bones in the foot. This is the case also with the 2 constant metatarsophalangeal sesamoid bones of the big toe. The point of time of the first appearance of these latter bones can be fixed on the basis of the following Table.

				373				
				372				
				370				
				274				
				267				
				184				
352				179				
350				324				
344				307				
216				285				
215				284		total		
181		368		162				
321		357		97				
247		356		169				
246		211		23				
225		340		346				
221		199		235				
204		172		218				
189		295		155				
180		258		42				
294	375	132		95				
131	369	135		4				
116	314	119		3				
125	231	79		306				
17	146	24		229				
weeks	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16

Italics indicate that the 2 constant sesamoid bones are not developed, thick types indicate that they are found in prochondral cartilage, and normal types that they are found in hyaline cartilage.

Thus the 2 constant sesamoid bones are laid down in 11 to 12 weeks old embryos. Definite signs of the presence of in-constant metatarsophalangeal sesamoid bones prove to be found only in embryos 12 to 13 weeks old or more. The inter-

¹⁾ By sesamoid bones shall be understood exclusively the plantar and dorsal metatarsophalangeal and interphalangeal sesamoid bones. (As for the term sesamoid bones used in a wider sense, see p. 207).

phalangeal sesamoid bones, on the other hand, are found in embryos 11 to 12 weeks of age. The difference is probably accidental.

For the sake of perspicuity I have divided the sesamoid bones in 3 subgroups, viz. a) the metatarsophalangeal, b) the interphalangeal, and c) the divided sesamoid bones.

a. Ossa Sesamoidea Metatarso-Phalangealia.

α Constant:

As already mentioned, there are found 2 constant, plantar sesamoid bones corresponding to the metatarsophalangeal joint of the big toe.

After the first development of these bones in 11 to 12 weeks old embryos I have found conditions deviating from the normal in 4 pairs of feet only. Thus in

65 (13 to 14 weeks): in the right foot a fibular sesamoid bone (normal), but no tibial; in the left foot a fibular bone half the normal size and a normal tibial bone.

109 (12 to 13 weeks): normal fibular and about half-sized tibial sesamoid bones in both feet.

301 (12 to 13 weeks): exactly like 109.

367 (14 to 15 weeks): normal fibular sesamoid bones and tibial bones ab. one-tenth the normal size in both feet.

β Inconstant:

In addition to the above 2 constant sesamoid bones on the plantar side of the metatarsophalangeal joint of the big toe I once (152 (13 to 14 weeks)) have found a *third plantar sesamoid bone*, present in both feet. It is found to lie distal to the 2 constant, and, unlike those, in the midline. It is well-developed and ab. half the size of the 2 normal constant sesamoid bones.

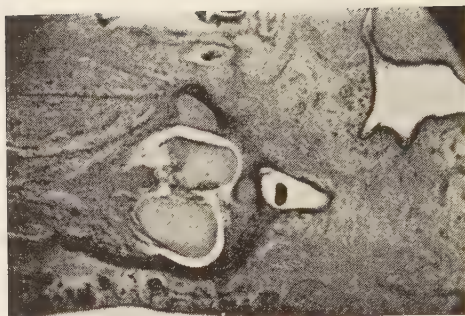


Fig. 75. 152 D (13 to 14 weeks). Section $15\ \mu$ thick, magnified 22 times. Slightly to the left of the middle of the picture we find the head of the 1st metatarsal consisting of 2 almost fused segments. The fibular constant sesamoid bone of the big toe is seen just above the head. To the right of these there is found in the midline an inconstant mesial sesamoid bone in the 1st metatarsophalangeal joint (visible in 8 sections, of which this is the 5th). In front of the latter we find the tendon of the flexor hallucis muscle.

Inconstant plantar sesamoid bones (corresponding to the 2 constant of the big toe) have been observed also in the other metatarsophalangeal joints. The following Table shows the pairs of feet in which sesamoid bones are found in the 2nd, 3rd, and 4th metatarsophalangeal joints.

IV		191		160		
	51	69		26		
III		69		26		
II		191	264			
	51	156	257	26	347	303
weeks	13-14	14-15	15-16	16-17	17-18	18-19

Sesamoid bones in the 2nd metatarsophalangeal joints are found only as tibial sesamoid bones, 7 times bilaterally (in one case of the size of the constant bones in the big toe, in the others smaller) and once unilaterally. The percentage frequencies can be calculated only on feet from embryos older than 12 weeks.

7 pairs and 1 single among 187 pairs: $4.3\% \pm 1.5$.

15 feet among 374: $4.0\% \pm 1.0$.

Sesamoid bones in the 3rd metatarsophalangeal joints are found only twice, both times unilaterally as tibial sesamoid bones (one right and one left). Percentage frequencies:

2 single among 187 pairs: $1.1\% \pm 0.8$.

2 feet among 374: $0.53\% \pm 0.4$.

Sesamoid bones in the 4th metatarsophalangeal joints are found only bilaterally; in 3 pairs of feet as tibial, and in 2 pairs as both tibial and fibular bones. Percentage frequencies:

5 pairs among 187 pairs: $2.7\% \pm 1.2$.

10 feet among 374: $2.7\% \pm 0.9$.

Sesamoid bones in the 5th metatarsophalangeal joints are found in the following pairs of feet:

				354													
		312	305	265	310												
		304	209	250	276												
		302	150	275	264	234											
		185	152	191	257	200	347										
		100	86	156	202	183	67										
		157	51	149	83	160	85	147									
		32	28	113	124	26	82	223									
	162	14	1	69	74	11	21	174									77
weeks	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	19-20	20-21	21-22	22-23	23-24	24-25	25-26	26-27	

The findings are bilateral in 42 cases, distributed as follows: 21 pairs present both tibial and fibular sesamoid bones (often the tibial bones differ in size from the fibular), 18 present only tibial bones, and 3 only fibular.

In 7 cases there is observed a difference between the two feet:

14: tibial bone bilateral, fibular only left,

69: tibial bone bilateral, fibular only right,

82: tibial bone only left, fibular only right,

83: tibial bone bilateral, fibular only left,

156: tibial bone bilateral, fibular only right,

200: tibial bone only left, fibular bilateral, and

77: tibial bone bilateral, fibular only left.

Tibial plus fibular sesamoid bones and tibial bones alone are thus found almost equally often; fibular sesamoid bones alone, on the other hand, are observed in a scant 8 per cent only.

The percentage frequencies of sesamoid bones in the 5th metatarsophalangeal joint are calculated at:

49 pairs among 187 pairs: $26.2\% \pm 3.2$.

98 feet among 374: 26.2% $\pm$ 2.3.

Percentage frequency for tibial sesamoid bones:

90 feet among 374: $24.1\% \pm 2.2$.

Percentage frequency for fibular sesamoid bones:

56 feet among 374: 15.0% $\pm$ 1.9.

cases — exclusively from feet of embryos older than 12 weeks, are as follows:

101 pairs and 7 single among 187 pairs: $57.8\% \pm 3.6$.

209 feet among 374: $56.0\% \pm 2.6$.

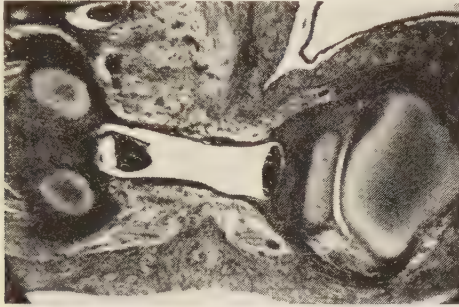


Fig. 76. 110 D (14 to 15 weeks). Section $20\ \mu$ thick, magnified 22 times. The picture shows from right to left: base of terminal phalanx of big toe, extra big hallucal interphalangeal sesamoid bone (found in 13 sections, of which this is the 5th), tendon of flexor hallucis muscle, and next the two constant sesamoid bones of the big toe (found in 19 sections. This is the 5th, where they have not yet reached their full sizes).

While in 106 of the pairs of feet the interphalangeal sesamoid bone in the big toe is single and mesial, (either bilaterally or unilaterally), conditions are somewhat different in the remaining 5 pairs. These pairs will be mentioned further in the following section (p. 80).

Sesamoid bones in the proximal interphalangeal joints of the 5th toes are found in the following pairs of feet:

	304			366			
	210		233	277	227		
	157		148	87	256		303
	101	51	149	83	142	82	223
weeks	12-13	13-14	14-15	15-16	16-17	17-18	18-19

Among these 18 pairs 16 have the sesamoid bone in both feet and 2 in the right foot only.

This gives the following percentage frequencies for feet from embryos older than 12 weeks:

16 pairs and 2 single among 187 pairs: $9.6\% \pm 2.1$.

34 feet among 374: $9.1\% \pm 1.5$.

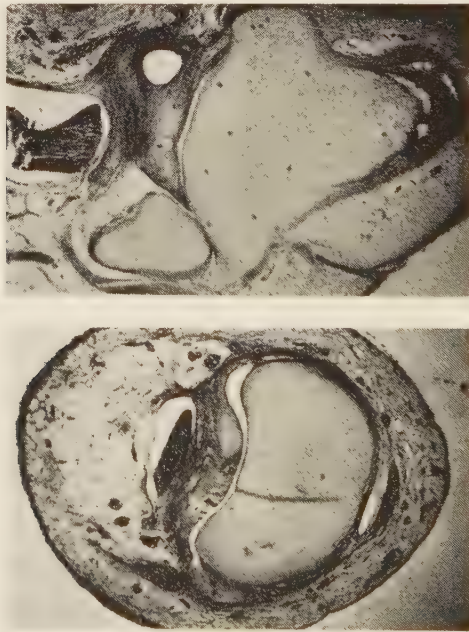
c. Ossa Sesamoidea Partita.

Among all the metatarsophalangeal sesamoid bones mentioned above, constant as well as inconstant, there is not found a single case of division of the cartilaginous primordium, not even the slightest suggestion of a division.

As for the interphalangeal sesamoid bones, observations made among those occurring in the big toes are suggestive that a sesamoid bone division may occasionally be congenital, i. e. be present at the hyaline cartilage stage. As mentioned p. 79, the interphalangeal sesamoid bone of the big toe is single and mesial in 106 pairs of feet, while conditions are different in the remaining 5. These 5 pairs will be described below.

277 (15 to 16 weeks): S: single, mesial siI; D: siI here likewise mesial, but almost completely bipartite in a tibial and a fibular half. The two halves together correspond in size to that in the left foot.

143 (16 to 17 weeks): D: siI is seen to be mesial, but almost completely bipartite in a smaller tibial and a bigger fibular



Figs. 77 and 78. 143, D and S respectively (16 to 17 weeks). Sections 10 μ thick, magnified 25 times. Fig. 77 shows a mesial, almost completely bipartite siI. Fig. 78 presents a decidedly fibular siI.

segment (Fig. 77); S: here there is only one sesamoid bone, which, however, is situated decidedly on the fibular side, and corresponds in size to the fibular segment in the right foot (Fig. 78).

160 (16 to 17 weeks): D: a tibial and a fibular siI, equal in size and separated completely by loose connective tissue (Fig. 79); S: no siI at all.

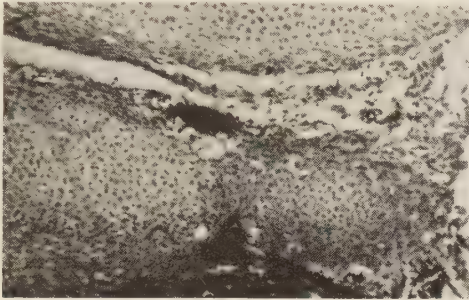


Fig. 79. 160 D (16 to 17 weeks). Section $10\ \mu$ thick, magnified well over 100 times. SiI completely separated in a tibial and a fibular segment. The phalanx is seen superiorly in the picture.

134 (15 to 16 weeks): D: the siI is situated decidedly on the fibular side, and there is no tibial segment; S: no siI at all.

20 (18 to 19 weeks): S: a tibial and a fibular siI, equal in size and completely separated. In addition, however, the tibial half is divided in 2 segments lying side by side, of which the medial is ab. one-third of the peripheral. Both are well-defined and regular (Figs. 80 and 81). The fibular half appears to be loosely constructed, has so to speak fallen apart in 4 fragments (Fig. 82). D: a single, mesial siI corresponding in size to one of those in the left foot.

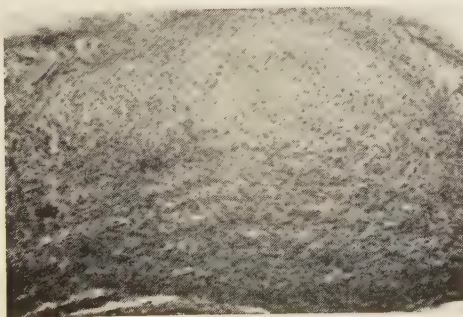
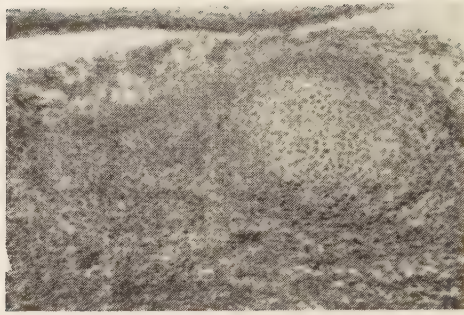


Fig. 80. See next Fig.



Figs. 80 and 81. 20 D (17 to 18 weeks). Sections $30\ \mu$ thick, magnified 100 times. In Fig. 80 the tibial half of the sil is seen to consist of 2 segments, the mesial being ab. one-third of the peripheral in size. Fig. 81 illustrates the conditions 4 sections later. The mesial segment of the tibial half of the sil is no longer visible.

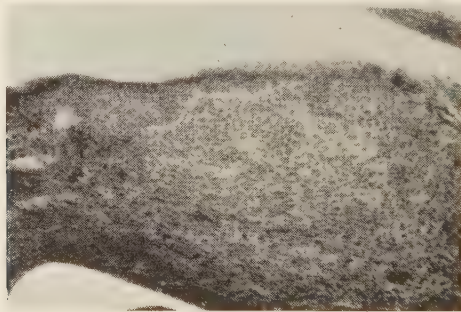


Fig. 82. 20 D (17 to 18 weeks). Section $30\ \mu$ thick, magnified 100 times. The fibular half of the sil is seen to be of a strangely loose construction, has so to speak fallen apart.

The percentage frequencies of divided interphalangeal sesamoid bones in the big toes, calculated for embryos older than 12 weeks, are as follows:

1 pair and 4 single among 187 pairs: $2.7\% \pm 1.2$.

6 feet among 374: $1.8\% \pm 0.7$.

8. *Os subfibulare.*

In one single case I find conditions suggestive of an independent primordium of an os subfibulare. That is in 195 (16 to 17 weeks), but only in the right foot. While the normal bone primordia have reached the cartilage stage, that of the accessory bone is partly in the cartilage stage and partly in the pro-chondral stage. The future bone is visible in 10 sections and is in all seen to be independent of the fibular malleolus. Be it

added, however, that the finding does not stand out so distinctly and indisputably as my other findings.

Percentage frequencies:

1 single among 250 pairs: $0.4\% \pm 0.4$.

1 foot among 500: $0.2\% \pm 0.2$.

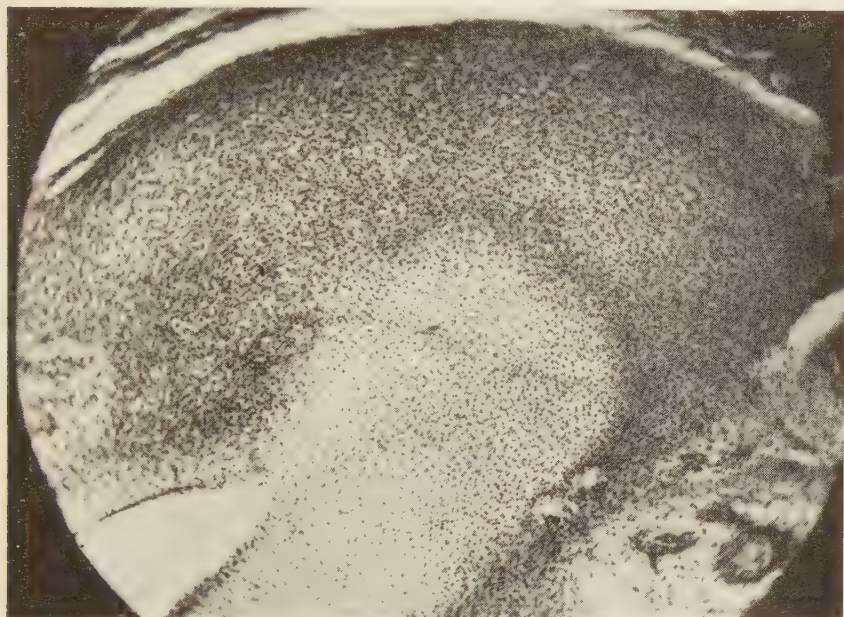


Fig. 83. 195 D (16 to 17 weeks). Section $20\ \mu$ thick, magnified 85 times. The fibular malleolus is seen to extend from the lower left side to the upper right. Above this there is found a spherical formation like a shell, consisting to the right of cartilage and to the left of prochondral cartilage, which latter fuses with the surrounding tissue. This os subfibulare is visible in 10 sections. The present is the 5th.

In several other cases the tip of the fibular malleolus is found independent in some sections, simulating an os subfibulare. But in these cases succeeding sections plainly show the element to be only the tip of the malleolus. The conditions correspond exactly to those observed for the os subtibiale, mentioned p. 90.

9. *Os tibiale.*

The os tibiale is found preformed in hyaline cartilage in the following pairs of feet:

	172	274			214	277		
	119	324	335		156	134		85
	79	235	268	353	123	87	84	82
weeks	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18

The os tibiale is by no means equally developed in both feet. It may be bigger in one foot than in the other, and it may be unilateral. It seems to be a characteristic feature of the os tibiale that it is situated in close relationship to the tibialis posterior tendon, close to the insertion of the latter on the navicular tuberosity (the distance from the navicular to the os tibiale is in none of my cases more than half the breadth of the navicular). The fibular portion of the os tibiale may, however, very well be clear of the tendon.

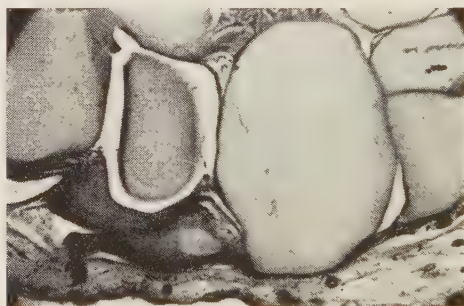


Fig. 84. 134 D (15 to 16 weeks). Section 20 μ thick, magnified 22 times. From left to right we find: calcaneum (v-shaped), tip of head of talus, navicular, followed by 3 cuneiforms. Inferiorly, between the head of the talus and the navicular a typical os tibiale is seen imbedded in the tendon of the tibialis posterior muscle. The os tibiale is visible in 10 sections, of which this is the 6th.

The os tibiale is in my material found to be bilateral 13 times and unilateral 6 times (4 right and 2 left), i. e. bilateral in 68 per cent. This gives percentage frequencies of:

13 pairs and 6 single among 250 pairs: $7.6\% \pm 1.7$.

32 feet among 500: $6.4\% \pm 1.1$.

The question of the presence of an os tibiale is, however, not settled by ascertaining whether or not such is found as an independent cartilaginous element. In some of the unilateral cases there proves to be a similar element also in the other foot,

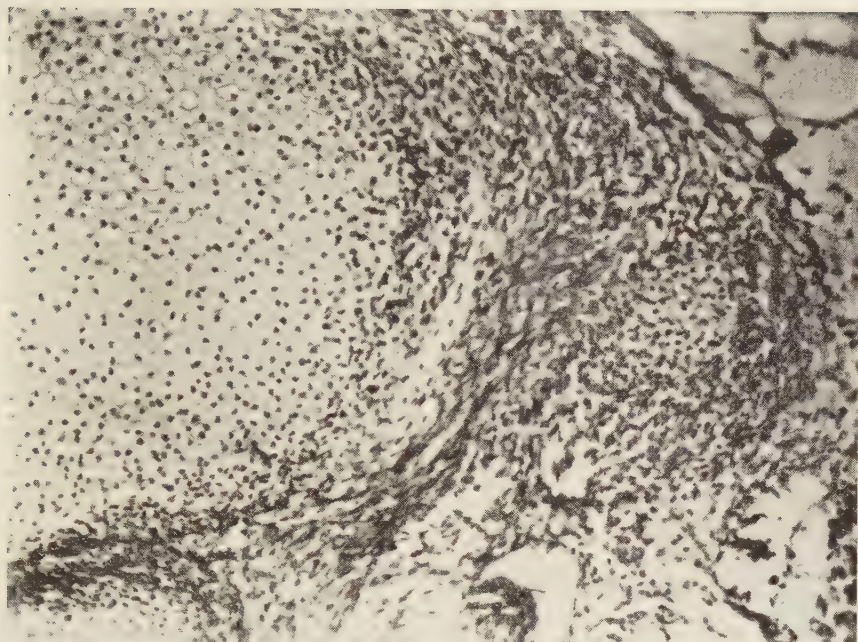
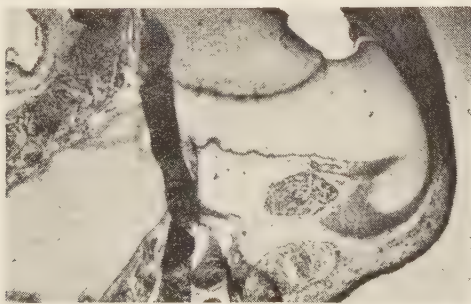
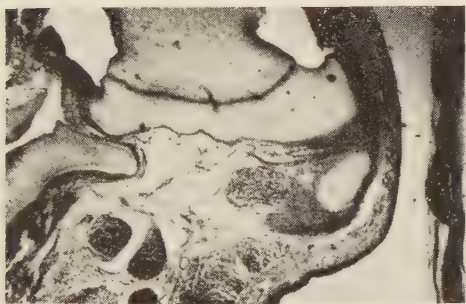


Fig. 85. 172 S (10 to 11 weeks). Section $10\ \mu$ thick, magnified 200 times. The navicular is seen to the left, and to the right the os tibiale imbedded in the tibialis posterior tendon. The os tibiale is visible in 13 sections, of which this is the 8th.

but here continuous with the navicular connected by a bridge. Thus, for instance, in 82 and 99:

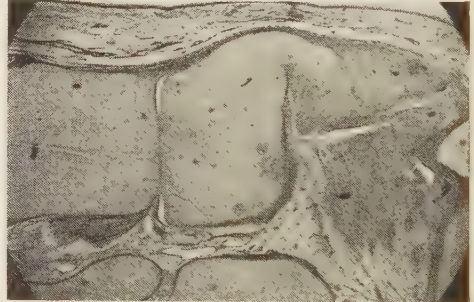
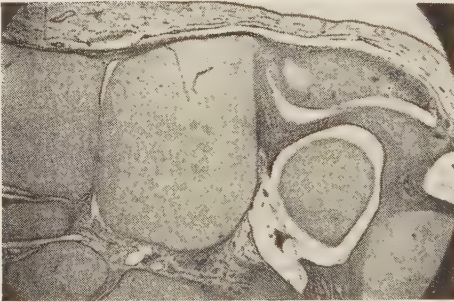
82 (17 to 18 weeks): D: big, distinct os tibiale, which, where



Figs. 86 and 87. 82 S (17 to 18 weeks). Sections $10\ \mu$ thick, magnified 22 times. The head of the talus is seen superiorly in the middle, after which follows the navicular. In Fig. 86 we find an apparent os tibiale (below and to the right of the navicular). Such is seen in 60 sections. This is the 54th. Fig. 87 shows the conditions 10 sections after Fig. 86. The beginning fusion between the supposed os tibiale and the navicular is here plainly visible.

closest to the navicular is removed from it by a half navicular breadth. S: 40 sections show an apparent os tibiale. Then the navicular turns up and these 2 formations are seen independent of each other in the next 20 sections (e. g. Fig. 86). In the sections following next the two bones are observed to have become connected by a bridge formation, which grows more and more massive (e. g. Fig. 87), so that 24 sections later the supposed os tibiale becomes continuous with the navicular.

99 (15 to 16 weeks): D: spur-shaped formation on the navicular in 17 sections (Fig. 89), after which the spur is seen to have been constricted off and be independent in 9 sections (Fig. 88). S: typical os tibiale in 40 sections. 2 sections after the os tibiale is no longer visible a small spur formation is seen on the navicular. This spur is present in 10 sections.



Figs. 88 and 89. 99 D (15 to 16 weeks). Sections 10 μ thick, magnified 22 times. Fig. 88 shows from left to right: tibial cuneiform, navicular, head of talus, and calcaneum. Superiorly, to the right of the navicular, we find an apparent os tibiale. The formation is visible in 9 sections. This is the 5th. Fig. 89 shows the conditions 12 sections proximal to Fig. 88. Here it is plainly seen that the supposed os tibiale is only a spur-shaped formation on the navicular. The spur is visible in 17 sections.

In other cases there is even found both a completely independent os tibiale and a spur formation, as for instance in 84 (16 to 17 weeks). Here the right foot presents a typical large os tibiale, seen in the first sections to be removed almost a whole navicular breadth from the navicular. In the succeeding sections the os tibiale comes nearer to the navicular, and a small spur develops on the navicular, as if a fusion were to take place (Fig. 90). Such fails to appear, however. The left foot reveals similar conditions: At first a large os tibiale alone in 21 sections, then side by side with the navicular in 38 sections,

but with no connection whatever. Then, 9 sections after the os tibiale has disappeared, a small spur is seen to develop on the navicular, corresponding to that seen in the right foot.

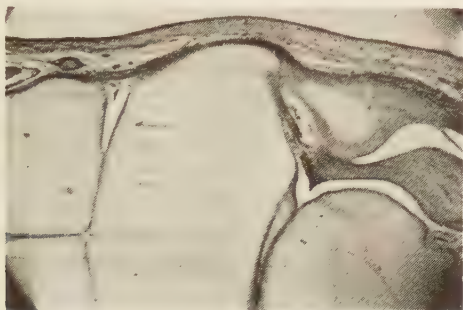


Fig. 90. 84 D (16 to 17 weeks). Section $10\ \mu$ thick, magnified 22 times. From left to right: tibial and intermediate cuneiforms, navicular, and head of talus. A large os tibiale is seen superiorly to the right of the navicular. Visible in 34 sections. This is the 27th. In addition a small spur-shaped formation is seen on the navicular. Visible in 25 sections, of which this is the 16th. The os tibiale never comes into contact with the spur formation. Finally a paracuneiform is seen above the tibial cuneiform. Visible in 19 sections, of which this in the 12th.

Finally, in a number of cases there is found only such a spur-shaped formation, now unilaterally and now bilaterally. The sizes of such spurs prove to range from barely visible to as big as that in 82 S (Fig. 87). In rare cases they may be awl-shaped, as in 282 (14 to 15 weeks) (Fig. 91).

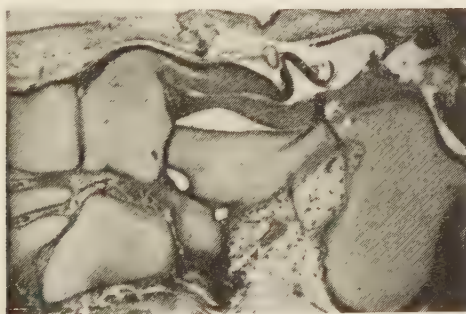


Fig. 91. 282 D (14 to 15 weeks). Section $10\ \mu$ thick, magnified 22 times. Superiorly in the middle we find the navicular, from the upper part of which an awl-shaped spur exits to the right, extending into the tibialis posterior tendon.

It appears from what has been stated above that the question of the presence of an os tibiale is a rather complicated one. It is not only a question of ascertaining whether or not the os

tibiale is present, but any transitional form from a large, distinct, independent os tibiale by spur to no spur seems to exist at the place of insertion of the posterior tibial muscle on the navicular.

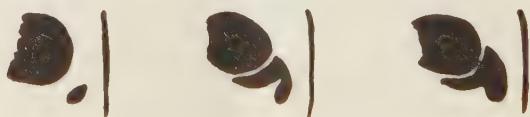
Therefore, in pronouncing on the percentage frequency of the os tibiale, one cannot feel perfectly satisfied with simply stating that it is 7 to 8 per cent. It is almost equally important to know how often there is found a spur, and how often there is found neither os tibiale nor spur. These questions are, however, somewhat difficult to answer quite precisely, because the spur is often only barely visible, perhaps even only in one foot, or one may consider it to be present in one foot simply because there is found a marked, well-developed spur in the other.

I have calculated the frequencies approximately and arrived at the following results:

No spur in ab. 46 per cent, small spur in ab. 18 per cent, and definite spur in ab. 28 per cent.

The age might be conceived to have a certain influence on these facts. However, this proves not to be so. Cases of os tibiale, spur, or neither are all represented in the different age groups. Only there is perhaps reason just to mention that among embryos aged 8 to 10 weeks none present os tibiale nor spur.

Finally mention will be made of the findings among the 25 left feet from normal, full-term, but still-born, children. In 2 cases, i. e. 8 per cent, there is found a large, distinct os tibiale. In both cases the fibular part of the os tibiale is clear of the



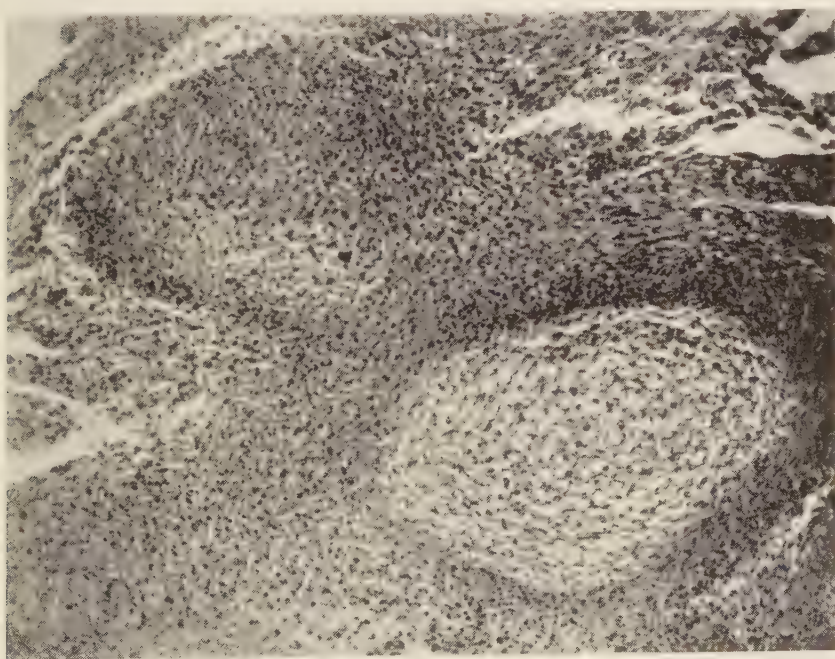
Figs. 92, 93, and 94 are diagrams based on frontal sections at right angles to the foot sole. Full size. Fig. 92 shows the talus to the left, and below there is seen an independent cartilaginous element, as it is found in 3 different feet. The line to the right is the tibial border of the foot. In more distal sections the independent formation disappears in 2 of the feet (450 μ and 600 μ further distally). These formations are in other words, typical beautiful ossa tibialia. In the 3rd foot the finding is different. Here they correspond to those illustrated in Fig. 92 over the first 300 μ , but then the navicular turns up between the talus and the element; and 150 μ further distally a fusion begins to take place between the elements and the navicular. Fig. 93 is an instance of this phenomenon. After another 150 μ the fusion is complete, as seen in Fig. 94. More distally still also the notch is planed out.

tibialis posterior tendon. Unquestionable spur is observed in 7 cases, i. e. 28 per cent.

The diagrams Figs. 92, 93, and 94 (full size) illustrate the position of the os tibiale as well as the spur formation.

10. *Is the calcaneum formed by fusion of 2 elements?*

In 3 cases (189, 246, and 247) the phenomena observed may favour the hypothesis that the calcaneum should have developed by fusion of 2 independent elements, a larger anterior and a smaller posterior, situated more on the plantar side. (The latter seems to be at a younger stage of development than the former). The findings are doubtful, however, since none of the three cases present 2 completely separated elements. The phenomenon is in all cases observed in the right foot, and the embryos are only 8 to 9 weeks old. 246 D illustrates the facts.



Figs. 95 and 96. 246 D (8 to 9 weeks). Sections 10 μ thick, magnified 200 times. Fig. 95 shows a large anterior calcanean element (inferiorly, to the right) and a smaller, situated behind and on the plantar side, which is at a younger stage of development (superiorly to the left). In Fig. 96 the 2 elements have become fused, though each element is still discernible. (The sections of this right foot do not run parallel to the foot sole, but somewhat obliquely).

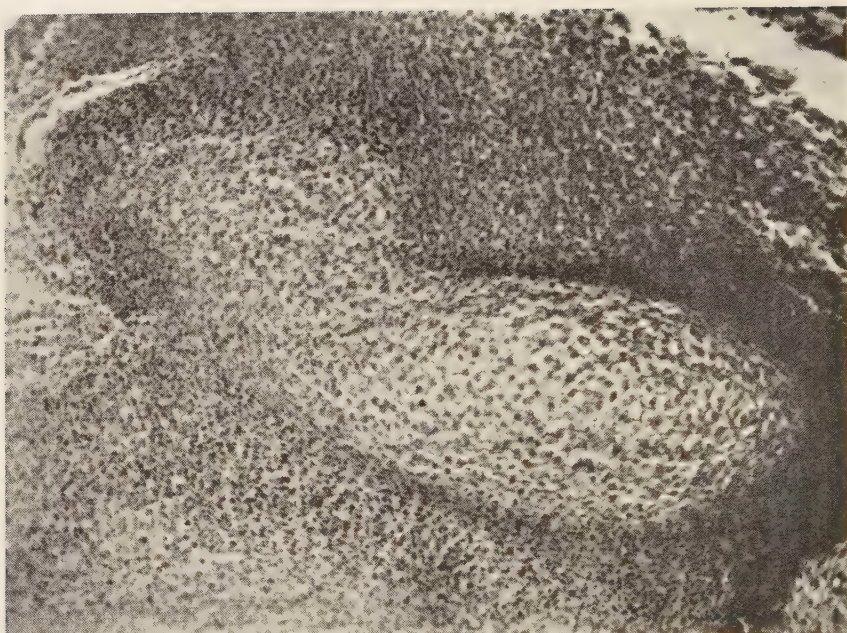


Fig. 96. See preceding Fig.

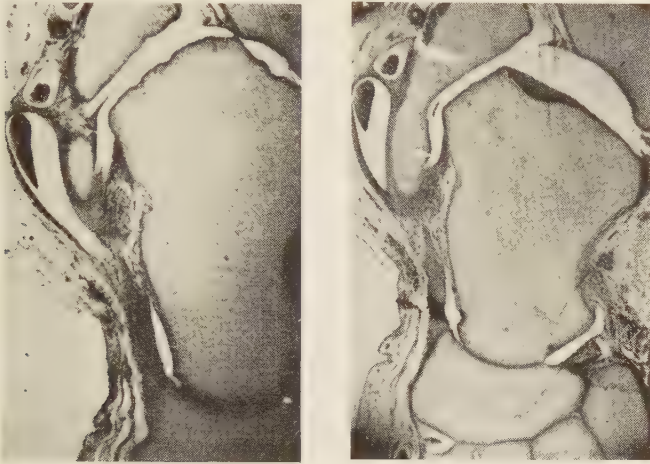
B. FALSE ACCESSORY BONES PREFORMED IN HYALINE
CARTILAGE, DISCLOSED BY SYSTEMATIC
SERIAL-SECTION ANALYSIS

In connection with the description of the accessory bones preformed in hyaline cartilage there is reason to mention some findings which might have been mistaken for future accessory bones occurring here as cartilaginous elements, if I had not undertaken a systematic serial-section analysis with examination of each individual section.

1. *Os subtibiale.*

The os subtibiale is in no case found as an independent cartilaginous element, but only as a seemingly independent formation. 194 D (13 to 14 weeks) and 137 S (19 to 20 weeks), are excellent examples of this fact. Both in the former right

foot and in the latter left foot a series of sections reveals an independent element below the tibial malleolus. But in both cases succeeding sections show the supposed independent formation to be only a process.



Figs. 97 and 98. 194 D (13 to 14 weeks). Sections $10\ \mu$ thick, magnified 22 times. 5 sections reveal an apparent os subtibiale (Fig. 97); but succeeding sections show this formation to be only the tip of the tibial malleolus manifesting itself as an independent bone in the first sections. Fig. 98 shows the conditions 5 sections distal to Fig. 97.

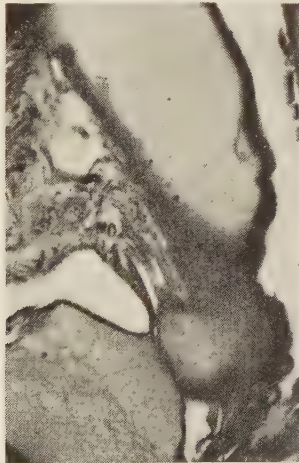
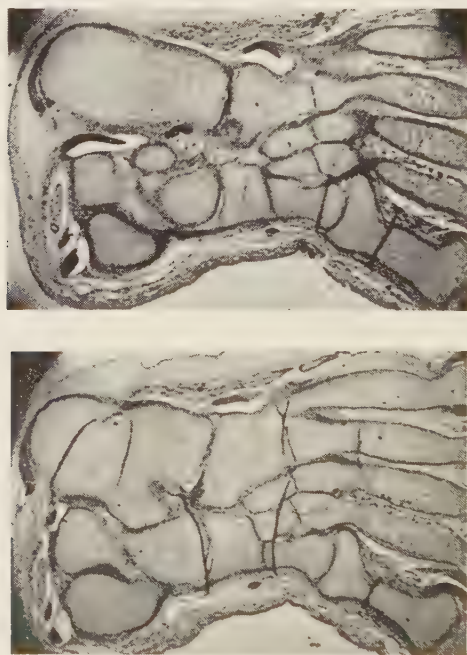


Fig. 99. 137 S (19 to 20 weeks). Section $25\ \mu$, magnified 22 times. Superiorly we find the tip of the tibial malleolus and below an apparently detached element. Below this again, to the left, the talus. Succeeding sections disclosed, however, fusion of the apparently independent element with the malleolus, just as was the case in 194 D.

2. *Os sustentaculi proprium.*

The os sustentaculi proprium is in no case found as an independent cartilaginous element but only as a seemingly independent formation. 172 (10 to 11 weeks) is an excellent example of this fact. Apparently independent ossa sustentaculi propria are seen here in some sections. But other sections show these apparently independent elements to be quite normal sustentaculi propria.



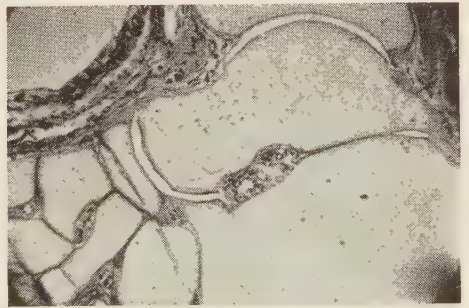
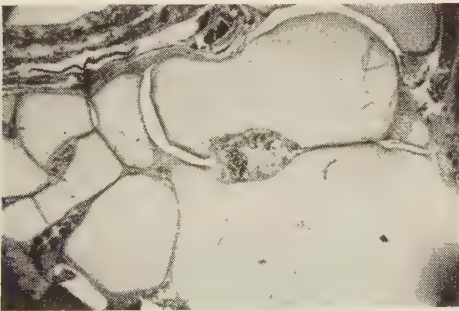
Figs. 100 and 101, 172 D (10 to 11 weeks). Sections 10 μ thick, magnified 22 times. Fig. 100 shows superiorly in a straight line from left to right: calcaneum, cuboid, 4th metatarsal. Below the calcaneum we find 4 cartilaginous elements situated like the ends of a cross. The superior end is an apparently independent os sustentaculi proprium. The inferior end is the tibia, and the 2 lateral ends the talus. Anterior to the head of the talus (the right end) we find first the navicular, then the tibial euneiform, and then the 1st metatarsal. The tendon of the flexor hallucis longus muscle is seen between the calcaneum and the apparent os sustentaculi proprium. This os sustentaculi proprium is present as an independent element in 10 sections, of which Fig. 100 is the 7th. Fig. 101 shows the conditions 6 sections after Fig. 100. Here it is plainly seen that the apparently independent element is no os sustentaculi proprium, but only a sustentaculum proprium manifesting itself as an independent formation in the first sections.



Fig. 102. 172 S (10 to 11 weeks). Section 10 μ thick, magnified 22 times. The picture shows from above downwards: tibia, talus, an apparently independent element, and calcaneum. Succeeding sections show — like in the case of 172 D — that the element is only the sustentaculum proprium beginning as an independent formation.

3. *Os trigonum.*

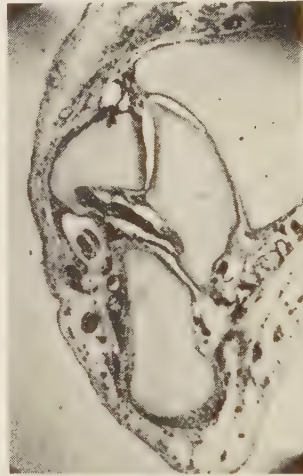
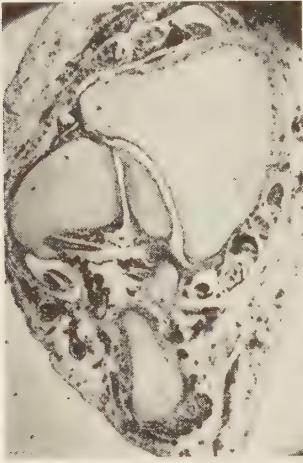
An os trigonum is in no case found as an independent cartilaginous element; but several of my series of sections show apparently independent formations. Thus, for instance, in 228 (13 to 14 weeks), where succeeding sections show the formation to be the fibular tubercle of the processus posterior tali, which



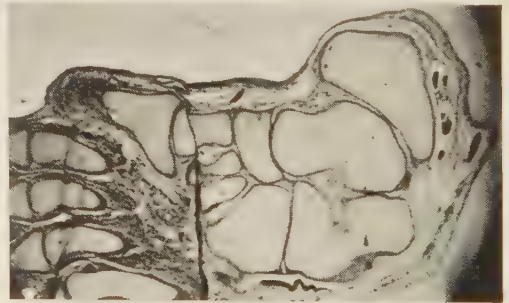
Figs. 103 and 104. 228 D (13 to 14 weeks). Sections 10 μ thick, magnified 22 times. *Fig. 103* shows from above downwards: tibia, talus, and calcaneum. Just behind the talus (to the right in the *Fig.*) there is seen a small triangular, independent element, corresponding exactly to an os trigonum. Such are the conditions in 9 sections, of which this is the 4th. Preceding sections show, however, that it is only the fibular tubercle of the processus posterior tali which has been constricted off.

Fig. 104, which shows the conditions 7 sections prior to *Fig. 103*, reveals this fact quite plainly.

seems independent at first, but which is later found to fuse with the rest of the talus. The apparent os trigonum may, however, also be part of the calcaneum, of which 368 D is an example.



Figs. 105 and 106. 228 S (13 to 14 weeks). Sections $10\ \mu$ thick, magnified 22 times. These Figures illustrate the same facts, but here in the left foot. Fig. 106 shows the conditions 4 sections after Fig. 105. In Fig. 105 the calcaneum is seen inferiorly, then follow the fibula to the left and the talus to the right, and finally superiorly, slightly to the left, the tibia. (Further, in both Figures we find the spur-shaped formation corresponding to the tip of the fibular malleolus.).

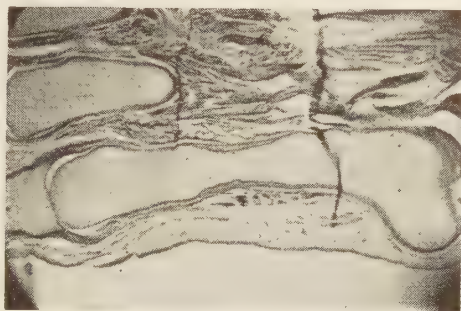
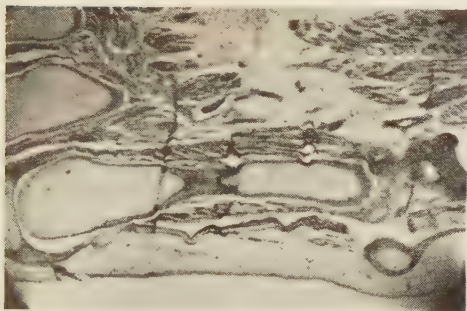


Figs. 107 and 108. 368 D (10 to 11 weeks). Sections $10\ \mu$ thick, magnified 22 times. In Fig. 107 one will likewise believe to have found an os trigonum. However, by systematic examination of the sections, this formation is found to be only a rest of the calcaneum. Fig. 108 shows the conditions 15 sections prior to Fig. 107. In Fig. 107 we find to the right from above downwards: the tibia, followed by a small corner of the fibula. The talus is seen in the next row, followed by a small corner of the calcaneum, the apparent os trigonum.

4. *Os Vesalianum*.

An *os Vesalianum* is in no case found as an independent cartilaginous element. But here, too, I have found apparently independent formations.

364 D (13 to 14 weeks) is an example of such an apparent *os Vesalianum*. In succeeding sections the formation is seen to fuse with the 5th metatarsal, forming the tuberosity of the latter. The section shows further how the abductor digiti quinti muscle inserts on the tuberosity. 223 D (18 to 19 weeks) shows another apparent *os Vesalianum*, large and distinct.



Figs. 109 and 110. 364 D (13 to 14 weeks). Sections $10\ \mu$ thick, magnified 22 times. Fig. 109 shows inferiorly, from left to right: base of proximal phalanx and 5th metatarsal. Below and to the right of the latter there is found an apparently detached cartilaginous element resembling an *os Vesalianum*. It is seen how the abductor digiti quinti muscle is inserted on this free element. Fig. 110, 9 sections later, does not show this free element, and the intermediary sections show that the apparent *os Vesalianum* actually is the tuberosity of the 5th metatarsal manifesting itself as an independent formation in the first sections.

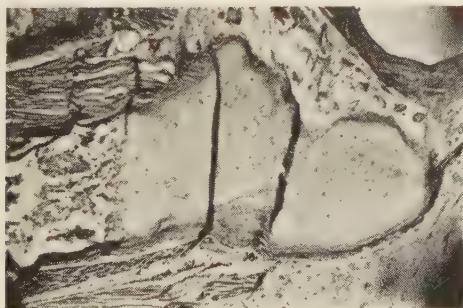


Fig. 111. 223 D (18 to 19 weeks). Section $10\ \mu$ thick, magnified 22 times. Similar conditions are seen in this picture. (The dark streaks are due to folds in the preparation).

C. SPUR-SHAPED FORMATIONS

Since spur-shaped formations have been mentioned several times above, it seems reasonable just briefly to state that such are also found elsewhere.

1. Tip of fibular malleolus of fibula:

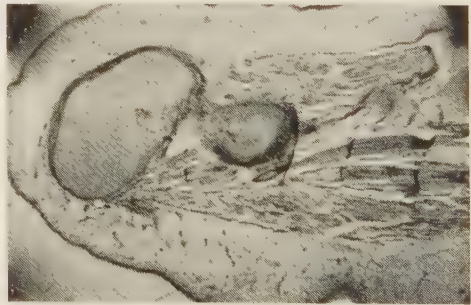
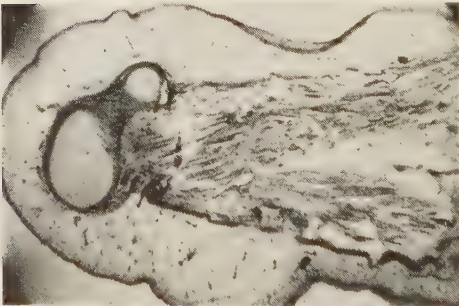
A spur-shaped process is often found here. Figs. 100 and 101 (p. 92) are histological pictures of such a process. I have never found this spur as an independent element.

2. Tip of tibial malleolus of tibia:

A spur-shaped process corresponding to that on the fibula is seen here in a few cases. This spur is not observed as an independent element either.

3. Fibular process of tuber calcanei.

The fibular process of the tuber calcanei is found to be strikingly long and detached in a very great number of cases. Thus, in nearly all the left feet it is seen to be constricted off and continue some way as an independent formation. In many — though not quite so many — right feet the anterior portion of the process is seen in the first sections as an independent element, but gradually as the sections proceed further dorsally the anterior independent portion is found to fuse with the root of the process. 290 D (12 to 13 weeks) and 139 S (15 to 16 weeks) are instances of this phenomenon.



Figs. 112 and 113. 290 D (12 to 13 weeks). Sections 10 μ thick, magnified 22 times. Fig. 112: this picture shows how the fibular process of the tuber calcanei apparently begins as an independent element (superiorly in the picture). But succeeding sections show fusion, as instanced in Fig. 113. In this picture there is seen an independent element just in front of the calcaneum, which, however, in succeeding sections proves to be only the anterior part of the calcaneum. Fig. 113 is 8 sections distal to Fig. 112.

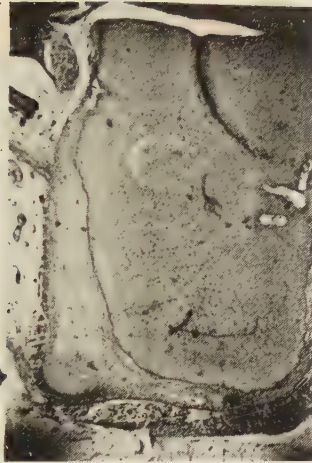


Fig. 114. 139 S (15 to 16 weeks). Section 10 μ thick, magnified 22 times. Here, too, the process is seen as an independent element (inferiorly to the left), but preceding sections shows it to be only a case of constriction.

4. Also elsewhere on the primordial bones of the foot we may find similar spur-shaped processes. Such findings are, however, single in the present cases and not particularly typical. Hence they will not here be described in detail.

D. OTHER FINDINGS

A brief account will be given below of various other findings — irrelevant to the present investigation — made during the histological examination of my embryos.

1. Synchondrosis between 2 cartilaginous elements.
2. Congenital crural defects and other crural anomalies.
3. Time of beginning ossification.

1. *Synchondrosis between 2 cartilaginous elements.*

Synchondrosis between 2 cartilaginous elements may extend over the entire area of contact between the 2 elements, or only over a larger or smaller part. A similar fusion of bones is not uncommon in adults (cf. *Pfitzner's* papers on this question). Here mention will be made only of the synchondroses found in own material.

a. Synchondrosis between talus and calcaneum:

is found bilaterally in 2 cases, 93 (12 to 13 weeks) and 162 (11 to 12 weeks). In both pairs of feet the fusion is seen tibially over the area of the proximal part of the sustentaculi tali calcanei.

b. Synchondrosis between calcaneum and navicular:

is observed unilaterally in 2 cases, 224 D (12 to 13 weeks) and 302 D (12 to 13 weeks). In both cases the synchondrosis is found at the point of contact between the anterior process of the calcaneum and the fibulo-planto-proximal corner of the navicular.

c. Synchondrosis between cuboid and navicular:

is found once, unilaterally, 83 D (15 to 16 weeks). The 2 elements have fused only planto-proximally.

d. Synchondrosis between navicular and tibial cuneiform:

is seen bilaterally in 3 cases, 135 (10 to 11 weeks), 367 (14 to 15 weeks), and 372 (11 to 12 weeks). The fusion is in all cases tibio-plantar, and most extensive in 367. In this pair there is found a minor fusion in the tibio-dorsal direction as well.

e. Synchondrosis between cuneiform and 3rd metatarsal:

is found in the following pairs of feet:

			103	364					
			32	348					
			22	51	214		165		303
	340	372	14	25	191	257	11		66
weeks	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19

The fusion is found bilaterally 11 times and unilaterally 6 times (3 in right foot and 3 in left). It is in all cases partial only, always on the plantar side, generally extending only over the plantar one-fourth or one-fifth, never more than one half. The percentage frequencies are calculated to be:

11 pairs and 6 single among 250 pairs: $6.8\% \pm 1.6$.

28 feet among 500: $5.6\% \pm 1.1$.

f. Interphalangeal synchondrosis:

is a phenomenon which is seen to vary greatly in frequency for the different phalanges of the individual toes. The fusion occurs most often between the medial and the terminal phalanges.

a. *Phalanges II + III digitus V* is found in the following pairs of feet:

			304										
			290										
			239					168					
			224					227					
			210			366	279						
			185	332	309	355	256						
			171	243	250	330	166						
			170	220	233	202	165						
			100	217	232	201	160						
			157	209	205	139	143		212				
	324	153	161	191	87	60		303					
	307	111	41	148	83	44		66					
	169	109	152	114	151	26	377	223			197		
	23	101	65	110	30	18	92	253			196		
135	3	93	51	70	29	11	136	63	137	68	72		
weeks	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	19-20	20-21	21-22	

In 70 cases the fusion is bilateral and in 9 unilateral (3 right feet and 6 left). The fusion is not seen to be of more frequent occurrence among the young than among the older embryos. A calculation of the percentage frequency of the fusion shall be based exclusively on embryos older than 12 weeks, for the phalanges do not attain their final shapes in cartilage till this point of time.

64 pairs and 9 single among 185 pairs: $39.5\% \pm 3.3$.

137 feet among 370: $36.0\% \pm 2.3$.

β . *Phalanges II + III digitus IV* is observed in 2 cases, 253 D (18 to 19 weeks) and 309 S (14 to 15 weeks), in other words, both times unilaterally. (The same embryos present bilateral fusion between medial and terminal phalanges of the 5th toe).

γ . *Phalanges II + III digitus III* is found in 1 case only, and only unilaterally, 65 S (13 to 14 weeks). (Here, too, there is found bilateral fusion between the medial and terminal phalanges of the 5th toe).

δ. *Phalanges I + II digitus III* is likewise found only once, 65 (13 to 14 weeks). The finding is bilateral.

ε. *Phalanges I + II digitus I* is seen in 2 cases. These findings will be further commented on, because the fusion is here of a peculiar character, being only partial and brought about by a tibial, plantar, spur-shaped process on the base of the terminal phalanx (*vide* p. 71). 28 (13 to 14 weeks) presents such a bilateral tibial fusion. On the fibular side there is only a spur. 329 (14 to 15 weeks) presents a similar fusion, but only in the right foot, and here, too, there is found a small spur on the fibular side (*vide* Fig. 71, p. 71). None of these 2 pairs of feet presents fusion between other phalanges.

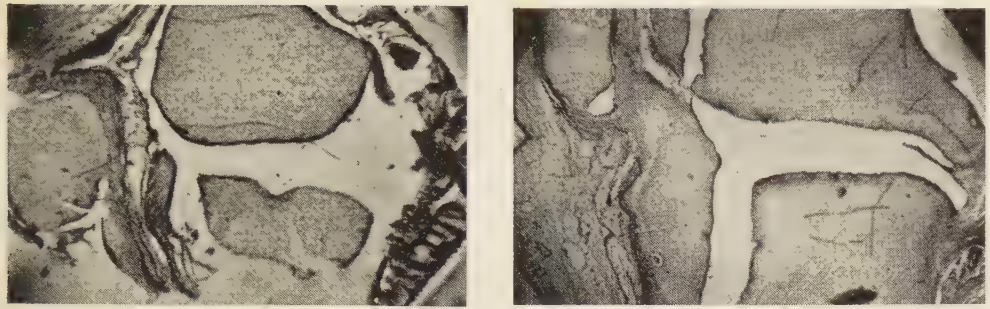
2. Congenital crural defect and other crural anomalies.

a. Congenital crural defect:

is found once. The tibia and the fibula are each divided in 2 segments with a line of division corresponding to the metaphysis. This finding is analogous to the congenital tibial pseudarthrosis well-known in children, which — despite its name — involves the fibula as well. My observation of this phenomenon is purely accidental, since, as a general rule, the feet are cut off proximal to the ankle joint. Hence the finding allows of no form of frequency calculation.

The observation has been made on 232 (14 to 15 weeks). In the right foot (where the sections have been cut at right angles to the longitudinal axis of the crus) the tibial epiphysis and some of the metaphysis are seen gradually to disappear, to be replaced successively by the rest of the metaphysis, but in such a manner that the two portions are never seen to come into contact with each other (Fig. 115). The fibula presents nothing extraordinary. Indeed, the distal portion disappears, but is not replaced by another (it has probably fallen out).

The left foot shows the phenomenon even more plainly (Fig. 116). Here the 2 fibular portions are seen to be slightly displaced in relation to each other and to have no points of contact whatever. The tibia appears as a completely regular continuous formation, i. e. has no cut surface, so there can hardly be any doubt that it is the distal portion. The proximal portion is never visible (must be supposed to have fallen out).



Figs. 115 and 116. 232 (14 to 15 weeks). Sections 15 μ thick, magnified 22 times. Fig. 115 (right foot) shows only the distal portion of the fibula, while of the tibia the 2 portions are seen quite independent of each other, the distal portion superiorly to the right, and the proximal portion inferiorly to the left. Fig. 116 shows the left foot. The 2 fibular portions are seen to the left in the picture, displaced *ad latus* and quite independent of each other (the same in all the other sections). Of the tibia only the distal portion is visible (superiorly to the right).

Finally the talus is seen inferiorly to the right.

b. Other crural anomalies:

In 2 cases, which have not been included in the present material, I have found other abnormalities. Thus, in one embryo, 16 to 17 weeks old, I have found absence of tibia and fibula unilaterally, as well as a deformed posterior foot, with ill-defined cartilaginous islands scattered irregularly about. In the other, 13 to 14 weeks old, the tibia is absent in one foot, and here, too, there are found irregularly scattered cartilaginous formations, but only round the ankle joint. I have not included these 2 cases in my material, because I have to do here with definite deformities.

3. Time of beginning ossification.

In the following it will just be stated at which point of time I have found the first traces of ossification in the different cartilaginous elements.

a. Calcaneum:

The primary ossification centre is not found till the 27th week (7th intra-uterine month).

In many cases I find a perichondrial ossification centre in-

constantly at a far earlier point of time. This centre is found in the following pairs of feet:

			234				
			256	342			
			200	192			
		276	165	92			
	156	87	122	140			197
	123	75	40	82	303		196
weeks	14-15	15-16	16-17	17-18	18-19	19-20	20-21

Only 2 of these findings are unilateral, both occurring in left feet (82 S and 342 S). The ossification is in all cases observed in the same place, that is fibularly, on the plantar side, just anterior to the base of the fibular process of the tuber calcanei.

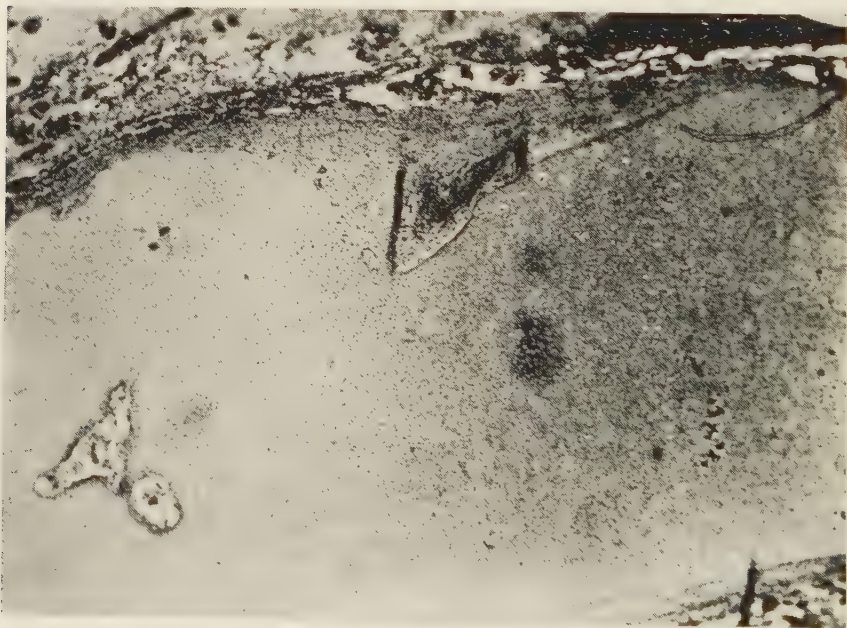


Fig. 117. 87 D (15 to 16 weeks). Section 10 μ thick, magnified 50 times. The perichondrial calcaneal centre is found superiorly in the picture. It is plainly seen to be situated further distally than the fibular process of the tuber calcanei (to the left in the picture). The perichondrial calcaneal centre is visible in 61 sections. This is the 8th. It does not increase in size in succeeding sections.

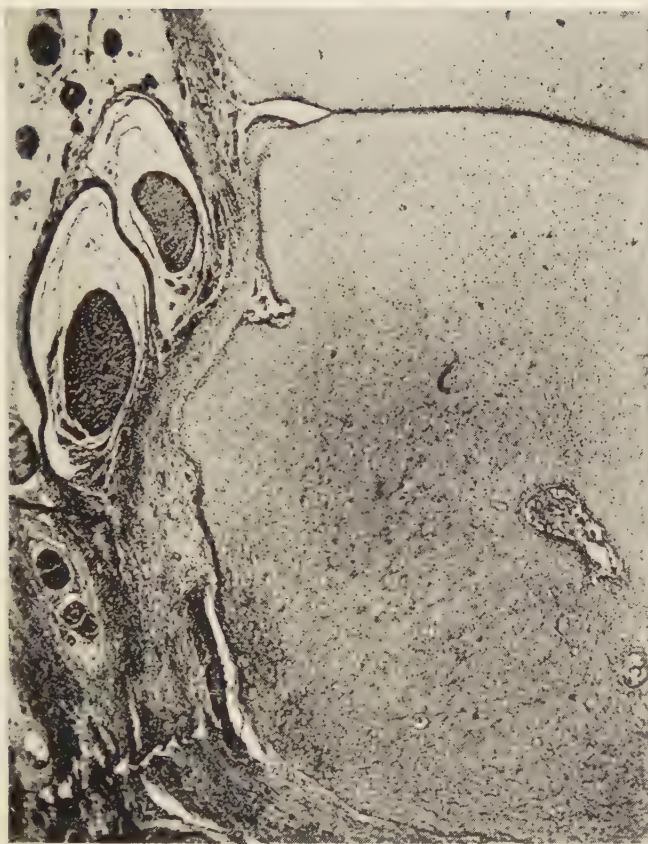


Fig. 118. 87 S (15 to 16 weeks). Section $10\ \mu$ thick, magnified 50 times. Here the perichondrial calcaneal centre is found situated on the fibular side of the calcaneum. Furthermore it is seen that the centre lies on the plantar side and in the same frontal plan as the trochlear process of the calcaneum, but more in the plantar direction. Superiorly to the left we find the tendons of the peronei in their respective tendon sheaths.

I have never observed this ossification centre in embryos before the 15th week. Within the 15th and 16th weeks it is found but rarely. Not till after the 17th week is the frequency of the same relative magnitude, whether we take the embryos week by week, or calculate the frequency on the basis of the total number of observed centres in all feet. The percentage frequencies can, therefore, be calculated only on the basis of embryos older than 16 weeks. They are as follows:

14 pairs and 2 single among 65 pairs: $24.6\% \pm 5.4$.

30 feet among 130: $23.1\% \pm 3.7$.

b. Talus:

The primary ossification centre is not found till the 27th week (7th intra-uterine month).

c. Metatarsals¹⁾:

I have found perichondrial ossification starting from the 11th week. The frequency is seen to be increasing from this age, and to comprise all embryos from the 14th week.

d. Proximal phalanges¹⁾:

The corresponding embryonic ages are here from the 14th and the 17th week respectively.

e. Medial phalanges¹⁾:

The first time I have found perichondrial ossification centres for these phalanges is within the 18th week. But not even in the oldest embryos examined (26 to 27 weeks) does the ossification comprise all these phalanges.

f. Terminal phalanges¹⁾ (including the terminal phalanx of the big toe).

Perichondrial ossification centres are seen to be present from the 11th week, and to comprise all embryos from the 15th week.

E. SEX INCIDENCE

The sex has been estimated only for embryos with foot lengths of 14 mm. or more, i. e. older than 14 weeks, because I dared not, without closer examination, pronounce with certainty on the sex in the cases of younger embryos.

122 embryos are over 14 weeks old. The genitals are included in 94 of these, while of the remaining 28 embryos only the feet or the lower extremities are available.

Of these 94 embryos 44 are female and 50 male, or 47 and 53 per cent respectively, with a standard error of 5.6. Accordingly we cannot conclude from the present material that male abortions are more frequent than female; but in 1947 I showed this to be the case, on the basis of a more comprehensive material (158 embryos, of which 44 per cent were female and 56

¹⁾ In practically all the embryos the tibial metatarsals and the phalanges have reached a more advanced stage of development than the fibular.

per cent male, with a standard error of 3.9, i. e. the difference was more than 3 times the standard error). The same observation has been made by other writers.

F. COMPARISON BETWEEN THILENIUS' AND OWN

EMBRYOLOGICAL MATERIALS

The only available embryological material of any size, comprising a number of accessory bones within a well-defined area, is that published by *Thilenius* 1896 dealing with the human hand. However, *Thilenius* does *not* seem to have made systematic serial-section analyses with examination of each individual section.

Thilenius examined 84 hands from 46 embryos with a view to sesamoid bones and 181 hands from 118 embryos with a view to accessory bones in and about the carpus. He claims to have found all the sesamoid bones and 13 of the 16 accessory bones in and about the carpus which are known to be present in the hands of adults.

Moreover, he declares that all the accessory bones occur far more frequently in embryos in the 3rd and 4th month than in adults. This difference is in his opinion due to the fact that many of the accessory bones present in embryos are destroyed again later, and, as regards the accessory bones in and about the carpus, also to the fact that in no small number of cases the accessory bones fuse with the constant bones, forming processes on the latter.

Finally *Thilenius* concludes that where accessory bones are found preformed in hyaline cartilage the findings are always bilateral, though generally with a difference between the two hands.

Thilenius has not examined the foot, but he states that 3 accessory bones have been investigated and the results published by *Bardeleben*. *Thilenius* continues (referring to *Bardeleben's* investigations), "Sie beziehen sich nur auf drei accessorischen Tarsalia, doch besteht kein Grund, welcher die Verallgemeinerung ihrer Ergebnisse auch auf die übrigen verhinderte". A typical sentence, which is worth noting, since numerous subsequent writers have concluded likewise. These writers, without first

testing the investigations made by others of a few accessory bones, are apt to let the results of such investigations apply to the entire number of accessory bones.

Although *Thilenius*' and own investigations comprise different regions they are comparable with regard to certain fundamental facts. Such a comparison shows that the results of *Thilenius*' investigations of the hand and mine of the foot are incompatible. I admit that I rely more on my own investigations than on those undertaken by *Thilenius*, partly because my material is larger, and partly — which is more important — because my results are based on careful systematic serial-section analyses with examination of each individual section. *Thilenius* does not mention this important question with a single word.

While *Thilenius* finds sesamoid bones more often in embryos than in adults, I have found the frequency figures to be fairly alike for the two groups (see frequency Table, pp. 20—21).

While *Thilenius* finds 13 of the 16 accessory bones in and about the carpus, and even more frequently so in embryos than in adults, I can draw no general conclusions regarding the foot, because some of the accessory bones in and about the tarsus are found only in embryos, while others are found only in adults, and others again almost equally often in embryos and adults. It is a relatively small number of the accessory bones present in adults which are laid down in embryos (see frequency Table, pp. 20—21). That *Thilenius* finds so many is no doubt due to the fact that his investigations are not systematic serial-section analyses (cf. my false accessory bones p. 90).

Finally *Thilenius* is not right either when he states that the accessory bones occurring as hyaline-cartilaginous elements always are bilateral. My frequent absolutely unilateral findings go definitely against this theory (e. g. os intermetatarsale I, p. 68).

G. TABULATION OF EACH PAIR OF FEET

The individual pairs of feet have been tabulated. The Table has been divided in 5 subgroups with 50 pairs in each. The 5 subgroups follow in the order in which the embryonic feet concerned were examined, while the embryos within each subgroup have been numerically arranged.

Information is given in the Table on the following facts for each pair of feet: No., foot length in millimetres, CR in millimetres, age in weeks (menstruation age), sex, and thickness of section in μ . Where nothing else is stated the sections are paraffin sections. Furthermore the accessory bones found in each pair have been indicated. If this indication is followed by D or S it means that the accessory bone concerned is unilateral, right or left respectively, while no letter means that the finding is bilateral. The figures in parentheses indicate the number of sections in which the accessory bone concerned is observed. Finally * means that the description of the bone is accompanied by a picture or pictures.

The CR is lacking in a number of cases, where only feet, lower extremities, or half embryos were at my disposal. The sex has been set out only for embryos more than 14 weeks old.

First 50 Pairs of Feet:

No.	Foot		CR	Age	Sex	μ	Accessory Bones
1.	13.0	—	?	13—14	o	20	sVf.
3.	7.0	—	?	11—12	o	15	int (13—20), sI prochondral cartilage.
4.	7.2	—	54	11—12	o	10	sI prochondral cartilage.
7.	16.5	—	100	14—15	o	20	siI.
11.	20.7	—	120	16—17	o	25	sVt.
14.	11.2	—	75	12—13	o	15	sVt, sVfS, siI.
15.	13.4	—	93	13—14	o	15	
16.	11.9	—	80	13—14	o	15	siI.
17.	4.4	—	30	8—9	o	10	÷ sI.
18.	20.7	—	120	16—17	o	25	siI.
20.	26.5	—	?	17—18	o	30	siID, siIpS*, calc.acc.D (12)*, intph.t*.
21.	26.0	—	130	17—18	o	30	sVt, sVf, paracun (4—7).
22.	9.4	—	65	12—13	o	10	
23.	7.2	—	52	11—12	o	10	
24.	6.1	—	40	10—11	o	10	int (8—20), ÷ sI.
25.	11.5	—	75	13—14	o	15	int (14—37)*, siI.
26.	21.5	—	?	16—17	o	25	siIt, sIIItS, sIVt, sIVf, sVt, siI, paracun (12—8).
28.	12.6	—	?	13—14	o	15	sVt.

No.	Foot	CR	Age	Sex	μ	Accessory Bones	
29.	18.0	—	?	15—16	o	20	siI.
30.	19.2	—	115	15—16	o	20	
32.	9.3	—	66	12—13	o	10	int (12—20), sVt.
33.	11.7	—	78	13—14	o	15	siI.
49.	9.3	—	65	12—13	o	10	
51.	13.2	—	84	13—14	o	15	sIIIt, sIVt, sVt, sVf, siI, sipV.
53.	12.5	—	83	13—14	o	15	siI, intph.fD.
55.	17.1	—	110	15—16	o	20	siI.
64.	19.8	—	125	15—16	o	20	
65.	12.3	—	83	13—14	o	15	÷ sIt.
69.	16.5	—	100	14—15	♂	20	sIIItD, sIVt, sVt, sVfD.
70.	15.6	—	90	14—15	♀	20	siI.
74.	18.2	—	?	15—16	♀	20	sVt, siI.
79.	5.6	—	42	10—11	o	10	int (9—12), ÷ sI, tib (4—3).
86.	11.9	—	70	13—14	o	15	sVt, sVf.
93.	9.4	—	65	12—13	o	10.	
95.	7.6	—	52	11—12	o	10	sI prochondral cartilage.
101.	10.0	—	60	12—13	o	15	sipV.
109.	10.2	—	65	12—13	o	15	
110.	16.5	—	95	14—15	♀	20	siI*.
111.	10.3	—	70	12—13	o	15	
113.	14.4	—	90	14—15	♂	15	sVt, sVf, siI.
114.	16.6	—	100	14—15	♀	20	siI.
117.	11.0	—	70	12—13	o	15	
119.	6.0	—	44	10—11	o	10	÷ sI, tib (4—7).
124.	19.9	—	110	15—16	♂	20	sVt, sVf, siI.
125.	3.8	—	25	8—9	o	10	÷ sI.
138.	16.2	—	?	14—15	o	20	
149.	14.0	—	90	14—15	♂	15	sVt, sVf, siI, sipV.
151.	19.6	—	?	15—16	♀	20	siID.
152.	13.0	—	90	13—14	o	15	sIm, sVt, sVf, siI.
169.	8.8	—	60	11—12	o	10	

Second 50 Pairs of Feet:

31.	11.4	—	70	12—13	o	10	
40.	22.2	—	?	16—17	o	10	
41.	11.1	—	85	12—13	o	10	int (13—20), siL.
42.	8.2	—	60	11—12	o	10	sI prochondral cartilage, cun.I bip.
44.	21.4	—	130	16—17	o	10	siL.
58.	18.0	—	110	15—16	♂	10	siL.
60.	22.1	—	130	16—17	♂	25	siL.
75.	19.8	—	113	15—16	♀	20	siL.

No.	Foot	CR	Age	Sex	"	Accessory Bones	
82.	23.5	—	130	17—18	♂	10	sVtS, sVfD, siI, sipV, tibD (14).
83.	18.5	—	100	15—16	♀	10	sVt, sVfS, siI, sipV.
84.	22.3	—	125	16—17	♂	10	siI, tib (34—59)*, paracun (19—12)*.
85.	23.0	—	130	17—18	♂	10	sVt, sVf, siI, tib (20—75).
87.	19.5	—	120	15—16	♀	10	sipV, tib (12—12), paracun (14—17).
88.	24.1	—	?	17—18	o	10	siID
97.	8.3	—	?	11—12	o	10	
99.	18.2	—	110	15—16	♂	10	siID, tibS (40).
103.	9.3	—	?	12—13	o	10	
122.	23.0	—	125	16—17	♂	10	
123.	16.2	—	?	14—15	♀	20	siI, tibS (8).
134.	18.4	—	110	15—16	♂	20	siIpD, tib (10—10)*, cun.I bip.
135.	6.0	—	40	10—11	o	10	÷ sI.
136.	23.5	—	?	17—18	♀	10	siI, paracun (18—16).
139.	19.0	—	120	15—16	♀	10	
140.	23.5	—	127	17—18	♀	10	per (15—9)*, siI.
141.	22.2	—	120	16—17	♀	10	siI.
142.	20.0	—	117	16—17	♂	10	siI, sipV.
143.	22.6	—	128	16—17	♂	10	siIp*, paracun (13—12).
144.	22.0	—	125	16—17	♂	10	
148.	16.5	—	100	14—15	♀	20	sipVD.
150.	11.5	—	75	13—14	o	10	sVt, sVf, siI.
153.	9.5	—	65	12—13	o	10	
155.	7.3	—	?	11—12	o	10	sI prochondral cartilage.
156.	14.6	—	93	14—15	♀	10	siItD, sVt, sVfD, tib (2—8).
157.	10.7	—	70	12—13	o	10	int (9—24), sVt, sVf, siI, sipV.
160.	22.0	—	?	16—17	o	10	siVt, siVf, sVt, sVf, siIpD*, cun.I bip.
161.	12.5	—	?	13—14	o	10	paracun (8—10).
162.	8.7	—	?	11—12	o	10	sVt, siI, paracun (7—8).
163.	14.0	—	?	14—15	o	15	intS (20).
165.	21.0	—	120	16—17	♀	20	siI.
166.	20.1	—	116	16—17	♀	20	siI.
twins { 177.	23.0	—	130	17—18	♀	20	siI.
178.	23.0	—	130	17—18	♀	20	siI.
183.	20.1	—	110	16—17	♂	20	sVt.
190.	10.7	—	70	12—13	o	10	paracun (4—4).
191.	15.2	—	?	14—15	o	20	siIt, siVt, sVt, sVf, siI.
194.	12.5	—	83	13—14	o	10	siI, paracun (8—6).

No.	Foot	CR	Age	Sex	μ	Accessory Bones
195.	20.5	— 125	16—17	♂	20	siID, subfib.D (10)*.
200.	20.0	— 115	16—17	♀	20	sVtS, sVf, siI.
201.	18.2	— 115	15—16	♂	20	
202.	19.0	— 120	15—16	♂	20	sVt, paracun (3—3).
Third 50 Pairs of Feet:						
67.	26.0	— 140	17—18	♂	30	celloidin, sVt, siI.
68.	33.9	— 160	20—21	♀	30	celloidin, paracun (14—9).
92.	25.3	— 132	17—18	♀	30	celloidin, siI.
100.	10.5	— 60	12—13	o	15	sVt, sVf.
116.	4.2	— 27	8—9	o	10	÷ siI.
131.	4.5	— ?	8—9	o	10	÷ siI.
132.	6.3	— 48	10—11	o	10	÷ siI.
137.	31.1	— 160	19—20	♂	25	siI.
170.	9.4	— 60	12—13	o	10	
171.	9.4	— ?	12—13	o	10	
182.	12.5	— 75	13—14	o	15	siID.
185.	9.8	— 70	12—13	o	15	sVt, siI.
192.	24.6	— ?	17—18	o	20	siI, paracun (8—10).
205.	14.5	— ?	14—15	o	20	siI.
206.	13.0	— ?	13—14	o	15	siI.
209.	13.6	— 80	13—14	o	15	int (5—11), sVt, sVf, siI.
210.	9.2	— 58	12—13	o	10	sipVD.
214.	16.4	— 95	14—15	♂	20	siI, tibD (2), intph.fS.
217.	13.9	— 90	13—14	o	15	siI, paracun (6—5).
218.	7.2	— 50	11—12	o	10	siI prochondral cartilage.
220.	11.4	— 75	13—14	o	10	
224.	10.6	— 70	12—13	o	10	
228.	11.5	— 75	13—14	o	10	
229.	7.3	— 50	11—12	o	10	÷ siI, cun.I bip., paracun (10—6).
232.	15.6	— 106	14—15	♂	15	
233.	16.4	— 95	14—15	♀	15	int (11—22), siI, sipV.
235.	8.0	— 55	11—12	o	10	siI prochondral cartilage, tib (8—14).
239.	11.0	— 80	12—13	o	10	siI.
240.	11.4	— 80	13—14	o	10	
243.	11.5	— 80	13—14	o	10	siI.
253.	30.0	— 170	18—19	♀	10	
256.	21.5	— 123	16—17	♂	10	sipV.
257.	17.5	— 102	15—16	♂	15	siIlt, sVt, sVf, siI, intph.fD*, paracun (4—3).
258.	6.5	— 45	10—11	o	10	÷ siI.
261.	30.0	— 155	18—19	♂	10	siI, paracun (49—27).

No.	Foot	CR	Age	Sex	μ	Accessory Bones
262.	29.5	—	155	18—19	♂	10 siI.
266.	10.0	—	65	12—13	o	10
275.	14.2	—	100	14—15	♀	10 sVf, siI.
277.	19.0	—	110	15—16	♂	15 siIpD, siIS, sipV, tib (2—8).
279.	21.0	—	115	16—17	♂	10
280.	22.5	—	120	16—17	♀	10
284.	9.0	—	60	11—12	o	10 siI, paracun (10—6).
285.	7.8	—	53	11—12	o	10
294.	4.2	—	29	8—9	o	10 ÷ siI.
295.	6.4	—	41	10—11	o	10 ÷ siI.
300.	14.5	—	90	14—15	♂	10
305.	12.2	—	?	13—14	o	10 sVt, siI, paracun (13—11).
307.	8.0	—	?	11—12	o	10 int (10—18).
319.	16.0	—	95	14—15	♂	10
324.	7.4	—	55	11—12	o	10 tib (4—5), paracun (14—8).

Fourth 50 Pairs of Feet:

63.	27.9	—	150	18—19	♂	50 celloidin, paracun (3—3).
66.	30.2	—	?	18—19	♂	30 celloidin, calc.acc. (3—10)*.
77.	52.1	—	?	26—27	o	50 celloidin, sVt, sVfS.
146.	5.4	—	35	9—10	o	10 ÷ siI.
154.	49.5	—	235	25—26	♂	50 celloidin, siI.
172.	6.9	—	43	10—11	o	10 ÷ siI, tib (5—13)*.
174.	28.0	—	145	18—19	♂	50 celloidin, sVt, paracun (8—3).
179.	8.5	—	63	11—12	o	10
180.	4.4	—	?	8—9	o	10 ÷ siI.
184.	8.5	—	58	11—12	o	10
189.	4.2	—	27	8—9	o	10 ÷ siI, calc.bip.D.
199.	6.6	—	?	10—11	o	10 ÷ siI.
204.	4.1	—	28	8—9	o	10 ÷ siI.
221.	4.5	—	34	8—9	o	10 ÷ siI.
223.	27.5	—	160	18—19	♀	10 sVt, sVf, siI, sipV.
225.	4.6	—	30	8—9	o	10 ÷ siI.
227.	20.0	—	115	16—17	♀	10 siI, sipV.
231.	5.0	—	33	9—10	o	10 ÷ siI.
234.	21.5	—	135	16—17	♀	10 int (30—88), sVt, siI.
238.	16.4	—	93	14—15	♀	10 siI.
246.	3.8	—	30	8—9	o	10 ÷ siI, calc.bip.D*.
247.	4.0	—	30	8—9	o	10 ÷ siI, calc.bip.D.
249.	15.1	—	90	14—15	♀	10 int (17—25).
250.	16.3	—	100	14—15	♂	10 intD (20), sVt, sVf, siI.

No.	Foot		CR	Age	Sex	μ	Accessory bones
252.	21.5	—	?	16—17	o	10	siI, paracun (27—20)*.
259.	15.8	—	?	14—15	o	10	paracun (25—10).
260.	30.0	—	155	18—19	♀	20	siI.
263.	25.0	—	135	17—18	♀	10	paracun (10—5).
264.	19.0	—	110	15—16	♀	10	sIIIt, sVt, sVf, siI, paracun (24—8).
265.	16.5	—	100	14—15	♂	10	sVf, siI, paracun (21—20).
268.	9.2	—	60	12—13	o	10	tib (5—15).
276.	19.0	—	110	15—16	♂	10	sVt, sVf.
281.	22.5	—	120	16—17	♀	10	siI.
282.	14.2	—	90	14—15	♀	10	siI.
283.	14.5	—	?	14—15	♂	10	siI.
290.	10.0	—	?	12—13	o	10	
301.	9.2	—	?	12—13	o	10	siI.
302.	10.0	—	?	12—13	o	10	sVt, siI, paracun (8—6).
303.	29.8	—	?	18—19	o	10	sIIIt, siI, sipV.
304.	10.6	—	?	12—13	o	10	sVt, siI, sipV.
308.	9.2	—	61	12—13	o	10	
310.	17.7	—	100	15—16	♂	10	sVt, siI.
312.	9.5	—	?	12—13	o	10	sVt, siI.
314.	5.0	—	?	9—10	o	10	÷ siI.
317.	13.7	—	?	13—14	o	10	
318.	16.5	—	100	14—15	♂	10	siI, paracun (15—10).
320.	26.1	—	135	17—18	♂	10	
321.	4.3	—	28	8—9	o	10	÷ siI.
336.	10.0	—	?	12—13	o	10	intD (10).
340.	6.0	—	45	10—11	o	10	÷ siI.

Fifth 50 Pairs of Feet:

72.	39.5	—	157	21—22	♀	50	celloidin, siI.
115.	25.9	—	140	17—18	♂	50	celloidin, siI.
147.	27.2	—	140	18—19	♂	50	celloidin, sVt, siI, paracun (7—3).
168.	22.2	—	?	16—17	o	50	celloidin, intS (3).
181.	4.2	—	?	8—9	o	10	÷ sI.
196.	34.5	—	160	20—21	♀	50	celloidin, siI.
197.	34.5	—	160	20—21	♀	50	celloidin, paracun (5—4)
211.	6.1	—	45	10—11	o	10	÷ sI.
212.	30.5	—	150	18—19	♀	50	celloidin, siI.
215.	4.2	—	28	8—9	o	10	÷ sI.
216.	4.0	—	25	8—9	o	10	÷ sI, cun.I bip.*
267.	8.0	—	58	11—12	o	10	int (21—25).
274.	9.0	—	60	11—12	o	10	tib (9—16).
306.	7.0	—	?	11—12	o	10	÷ sI.

No.	Foot		CR	Age	Sex	μ	Accessory Bones
309.	16.2	—	95	14—15	♂	10	siI.
327.	15.0	—	85	14—15	♀	10	siI.
329.	14.7	—	90	14—15	♂	10	siI.
330.	18.0	—	100	15—16	♀	10	int (21—30), paracun (15—19).
332	12.9	—	?	13—14	o	10	siI.
335.	10.4	—	?	12—13	o	10	tibD (5).
337.	14.0	—	85	14—15	o	10	
338.	10.0	—	65	12—13	o	10	siI.
339.	11.0	—	80	12—13	o	10	intD (19).
341.	27.0	—	145	18—19	♀	10	siI.
342.	24.0	—	130	17—18	♂	10	siI.
343.	30.0	—	165	18—19	♂	10	
344.	3.8	—	25	8—9	o	10	÷ sI.
346.	7.1	—	?	11—12	o	10	sI prochondral cartilage.
347.	25.5	—	?	17—18	o	10	sIIIt, sVt, sVf, siI, paracun (18—16).
348.	13.5	—	85	13—14	o	10	cun.I bip*.
350.	4.5	—	28	8—9	o	10	intD (5)*, ÷ sI.
352.	4.5	—	?	8—9	o	10	÷ sI.
353.	12.5	—	?	13—14	o	10	tibD (6).
354.	14.5	—	?	14—15	o	10	sVt, sVf, siI.
355.	17.0	—	?	15—16	o	10	intph.t*.
356.	6.5	—	?	10—11	o	10	÷ sI.
357.	5.5	—	?	10—11	o	10	÷ sI.
358.	12.5	—	?	13—14	o	10	
361.	15.6	—	100	14—15	♂	10	siI.
364.	12.0	—	?	13—14	o	10	
366.	17.5	—	?	15—16	o	10	siI, sipV.
367.	16.2	—	95	14—15	♂	10	siI.
368.	6.2	—	45	10—11	o	10	÷ sI.
369.	5.4	—	?	9—10	o	10	÷ sI.
370.	9.0	—	?	11—12	o	10	siI.
372.	7.7	—	50	11—12	o	10	
373.	8.8	—	55	11—12	o	10	
374.	12.1	—	70	13—14	o	10	
375.	5.3	—	35	9—10	o	10	÷ sI.
377.	25.0	—	140	17—18	♀	10	siI.

H. SURVEY OF THE PERCENTAGE FREQUENCIES OF OBSERVED PRIMORDIAL ACCESSORY BONES IN EMBRYOS

The above tabulation will now be followed by a survey of the frequency figures calculated for accessory bones preformed as independent cartilaginous elements.

Of the 35 accessory bones described in this work (cf. p. 19), which are present in adults, 11 are found preformed in hyaline cartilage, i. e. 31.5 per cent. The percentage frequencies for these 11 are, however, not the same as for the corresponding bones in adults (see later).

Accessory bones preformed in hyaline cartilage are seen in 163 out of 250 pairs of feet, i. e. ab. 65 per cent. This percentage figure is actually too low, because the sesamoid bones are not definitely laid down till after the 12th embryonic week. If this fact is taken into account, the frequency is 146 accessory bones among 187 pairs of feet, or 78 per cent.

It will, therefore, be natural to divide the accessory cartilaginous elements in two groups: *A*: accessory bones in and about the tarsus, which are laid down simultaneously with tarsus and metatarsus, thus being found in embryos older than 8 weeks. *B*: accessory bones about the metatarsophalangeal and interphalangeal joints (in other words chiefly sesamoid bones), which are laid down simultaneously with the two constant sesamoid bones, thus being found after the 12th embryonic week.

The 187 pairs of feet from embryos older than 12 weeks with 78 per cent accessory bones preformed in hyaline cartilage are distributed as follows:

18 pairs present accessory bones all belonging to group A:	9.6%
87 pairs present accessory bones all belonging to group B:	46.5%
41 pairs present both A and B:	21.9%
41 pairs present neither A nor B:	22.0%
Bones of group A are found in 59 pairs of feet:	31.5%
Bones of group B are found in 128 pairs of feet:	68.4%

The A-group being laid down simultaneously with the tarsus and metatarsus primordia, the frequency for A could be calculated from the 250 pairs. This frequency is found to be 29.2 per cent, A being present in 73 pairs of feet. In 7 of these pairs there are found 2 accessory elements of group A, while the other pairs present only one each.

Of the 128 pairs of feet containing accessory elements belonging to group B, 45 present 2 or more cartilaginous elements of group B, while the others have only one each.

Thus, *my embryological foot-material shows:*
that accessory bones preformed in hyaline cartilage are found in nearly 80 per cent distributed as follows:

nearly 10 per cent exclusively in and about the tarsus,
 well over 45 per cent exclusively about the metatarso-
 phalangeal and interphalangeal joints,
 and 22 per cent of both categories;
and that only well over 20 per cent present exclusively constant bone elements preformed in hyaline cartilage.

It is interesting to see that these figures for my embryos accord with corresponding figures for adults, calculated a. o. by *Burman & Lapidus 1931*, who find accessory bones in 75 per cent, and *Geist 1914*, who finds accessory bones in and about the tarsus in 30 per cent.

Nevertheless the figures for the embryological and the adult materials are not comparable because of differences with regard to the kinds of accessory bones represented in the two materials. Thus, the os cuneiforme I bipartitum, the os interphalangeale, and the os paracuneiforme constitute from rather great to great percentages in the embryological material, whereas their numbers are extremely small or nil in the adult material. The reverse is the case with the os peroneum and the os trigonum.

Chapter 3.

OTHER WRITERS' HISTO-EMBRYOLOGICAL INVESTIGATIONS OF HUMAN AND ANIMAL MATERIALS

In this chapter mention will be made, as a supplement, of the various writers who have occupied themselves with histo-embryological investigations of human and/or animal embryos¹); and a survey will be given of their publications (which I have later employed). For each animal order some few of the most characteristic investigations will be discussed further.

I. MAMMALS.

A. HOMO SAPIENS (MAN).

Henke & Reyher 1874, *Bardeleben* 1883, 1884, and 1885, *Retterer* 1884, *Baur* 1886, *Leboucq* 1886, *Chemin* 1896, *Schomburg* 1900, *Bardeen* 1905, *Hasselwander* 1914, *Straus* 1927, *Hintzsche* 1930, *Francillon* 1933, *Schmidt-Ehrenberg* 1942.

Only *Bardeleben*, *Schomburg*, *Hasselwander*, and *Francillon* deal with the question of accessory bones. The other writers find only constant bones, even though they often examine embryos from the earliest stages of development of the extremital skeleton.

Bardeleben 1885 found the following independent elements:

T			F		
m?					
			tp ₃	tp ₆	
			tp ₂	tp ₅	
			tp ₁	tp ₄	
tp ₀		c ₁	c ₂	c ₃	
td ₀	td ₁	td ₂	td ₃	td ₄	td ₅
					mt _{VI} ?
mt ₀	= I	II	III	IV	V

¹) The animals are in all cases called by the Latin names applied by the author concerned. A list is found p. 12 indicating the English and the Danish name for the animal in question.

The tibial malleolus (= m) occurs possibly as an independent formation.

The talus is probably formed of 2 elements, viz. tp_2 = tarsale proximale 2 (= i_1 = intermedium 1) forming the body and tp_1 = tarsale proximale 1 (= t = tibiale) forming the head. Furthermore the tp_3 = tarsale proximale 3 (= i_2 = intermedium 2 = trigonum) fuses in most cases with these elements forming the processus posterior tali (*vide* criticism p. 173).

The calcaneum consists of 2 elements, an anterior tp_4 = tarsale proximale 4 (f = fibulare) and a posterior tp_5 = tarsale proximale 5. The latter consists probably again of 2 elements, since the posterior epiphysis must be supposed to have been formed of tp_6 = tarsale proximale 6.

The navicular consists of 2 elements situated side by side, the tp_0 = tarsale proximale prehallucis, forming the navicular tuberosity and the c_1 = centrale 1, forming the rest of the navicular.

The tibial cuneiform consists of 2 elements, the td_0 = tarsale distale prehallucis, forming the plantar half and the td_1 = tarsale distale 1, forming the dorsal half (see also foot-note p. 169).

The fibular cuneiform consists of 2 elements, the c_2 = centrale 2, forming the proximal minor portion (triangulare tarsi), and td_3 = tarsale distale 3, forming the rest.

The cuboid is in *Bardeleben's* opinion developed from 3 elements, viz. c_3 = centrale 3, forming the proximal portion, as well as td_4 = tarsale distale 4 and td_5 = tarsale distale 5, each forming its part of the distal portion.

The tibial end of the 1st metatarsal is supposed to be formed of the mt_0 = metatarsus 0 (prehallux), while the rest is formed of I = os metatarsale I.

The tuberosity of the 5th metatarsal is possibly formed of mt VI = os metatarsale VI.

With regard to the development of the proximal tarsal bones *Bardeleben* advances different opinions in his different papers. These opinions will be rendered here.

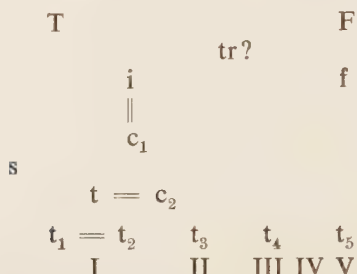
1883: The talus is formed of the proximal i = intermedium and the distal t = tibiale; the calcaneum of f = fibulare, excluding the tuber, which develops from the 6th ray; and the navicular is formed of c = centrale.

1885: The talus is formed of the proximal i = intermedium

and the distal c_1 = centrale 1; the calcaneum is formed of f = fibulare; and the navicular is formed of t = tibiale (i. e. the tuberosity) and c_2 = centrale 2 (i. e. the rest).

1894: The talus is formed of the proximal f = fibulare and the distal i = intermedium; the calcaneum is formed of pm = postminimus; and the navicular is formed of t = tibiale (i. e. the tuberosity) and c_1 = centrale 1 (i. e. the rest).

Schomburg 1900 found the following independent elements by examining 23 embryos:



At the prochondral stage the talus proves to be formed of 2 equally large elements situated one behind the other (i = intermedium and c_1 = centrale 1). It is not quite evident whether he found 2 elements at the cartilage stage (see criticism p. 174).

The calcaneum is formed of f = fibulare. Whether the sustentaculum tali is formed as an independent element is a question which he cannot definitely settle.

The navicular consists at the prochondral stage in half of the cases of a fairly large dorsal element (c_2 = centrale 2) and a smaller plantar element (t = tibiale), which fuse within the first part of the cartilage stage. In addition he once found an independent cartilaginous element (s) in the tendon of the tibialis posterior muscle, tibial to the navicular. He explains this bone as a sesamoid bone.

The tibial cuneiform consists at the prochondral stage in half of the cases (same as for the navicular) of a dorsal (t_2 = tarsale distale 2) and a plantar (t_1 = tarsale distale 1) element. The line of division between these 2 elements continues direct from the 2 elements of the navicular.

The cuboid is formed of one element only (t_5 = tarsale distale 5). Primarily this element articulates only with the 4th metatarsal; but secondarily also with the 5th metatarsal.

B. PRIMATES (ANTHROMORPHOID MONKEYS):

Retterer 1884 (hylobates).

Hylobates spec.:

Retterer 1884 found the following independent elements:

T		F	
	ta		ca
	nav		
c _I	c _{II}	c _{III}	cub
I	II	III	IV V

C. PROSIMIAE (DEMIMONKEYS):

Henckel 1930 (tarsius spectrum).

Schmidt-Ehrenberg 1942 (microcebus myoxinus Ptrs.).

Tarsius spectrum:

Henckel 1930 found the following independent elements:

T		F		(adult)	T	=====	F	
	ta		ca				ta	ca
	nav						nav	
c _I	c _{II}	c _{III}	cub		c _I		c _{II}	c _{III} cub
I	II	III	IV V		I		II	III IV V

The 5th metatarsal articulates at early stages with the fibular border of the cuboid; but not till later stages with the distal surface.

Nothing is stated about t_5 = tarsale distale 5.

Microcebus myoxinus Ptrs.:

Schmidt-Ehrenberg 1942 found the following independent elements by examining 4 embryos:

T		F		(adult)		T	F	
							ta	ca
i		f						
ctp		pi					nav	
ctd = cfd						c _I	c _{II} c _{III}	cub
t ₁	t ₂	t ₃	t ₄			I	II	III IV V
I	II	III	IV V					

The talus consists of 2 elements explained as *i* = intermedium and *ctp* = centrale tibiale proximale.

The calcaneum is formed mainly of *f* = fibulare. But on the proximo-plantar side there is found a tissue complex, explained as *pi* = pisiforme.

The navicular is formed of *ctd* + *efd* (= centrale tibiale distale plus centrale fibulare distale).

t = tibiale is found as prochondral cartilage in close relationship to the tip of the tibial malleolus.

The 5th metatarsal is not developed from *t* = tibiale distale 4 at the early stages. This is a secondary phenomenon.

D. RODENTIA (RODENTS):

Retterer 1884 (*cavia cobaya* — *mus rattus* — *lepus cuniculus*).

Baur 1885 and 1886 (*cavia cobaya* — *lepus cuniculus* — *erethizon dorsatus epixanthus*).

Emery 1894—1897 (*mus decumanus*).

Schmalhausen 1908 (*mus rattus*).

Holmgren 1933 (*mus musculus*).

Petri 1935 (*cavia cobaya*).

Schmidt-Ehrenberg 1942 (*mus musculus* L. — *citellus citellus* L. — *sciurus vulgaris* L. — *cavia porcellus* L.).

Mus decumanus:

Emery 1894—1897 found the following independent elements:

T	F
	ta ca
t	
	nav
ph	
t ₁ t ₂ t ₃	cub
I II III IV V	

Mus rattus:

Schmalhausen 1908 found the following independent elements:

T	F
	a ca
t	
	nav
ph	
t ₁ t ₂ t ₃	cub
I II III IV V	

The astragalus is probably formed of $i + cpr$ (= intermedium plus centrale proximale).

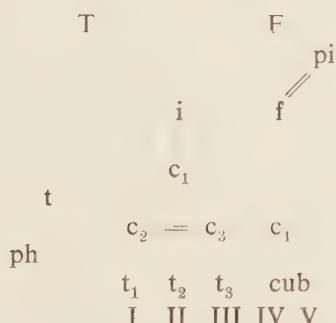
The navicular is supposed to be formed of $cd_2 + cd_3$ (= centrale distale 2 plus centrale distale 3).

The cuboid is supposed to be formed of $t_4 + t_5$ (= tarsale distale 4 plus tarsale distale 5).

t = tibiale remains independent in adults: Accessorium tibiale.

Mus musculus:

Holmgren 1933 found the following independent elements:



$i + c_1$ (= intermedium plus centrale 1) form the astragalus; $f + pi$ (= fibulare plus pisiforme) form the calcaneum, to which c_4 = centrale 4 later fuses.

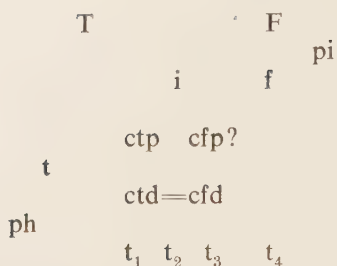
The navicular is formed of $c_2 + c_3$ (= centrale 2 plus centrale 3), two elements lying side by side.

t = tibiale forms the so-called accessorium, to which ph = prehallux is attached.

Holmgren states about the cuboid that it is developed from $t_4 + t_5$ (= tarsale distale 4 plus tarsale distale 5) ("in early stages of development five tarsals are present, one for each metatarsal. But the tarsalia 4 and 5 fuse already as blastemas"). It does not appear from the description, however, whether he has ocular evidence for the fact.

Mus musculus L.:

Schmidt-Ehrenberg 1942 found the following independent elements:



Later *i* = intermedium and *ctp* = centrale tibiale proximale fuse to form the talus. Similarly *f* = fibulare and *pi* = pisi-forme fuse to form the calcaneum.

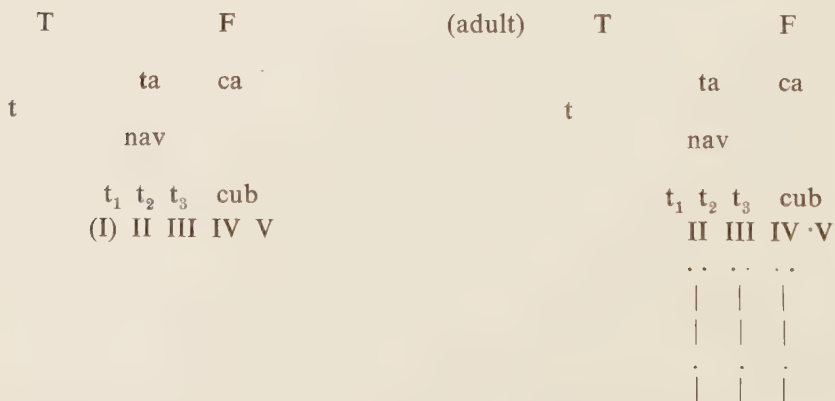
The navicular is plainly seen to have developed from 2 equally large elements situated side by side, *ctd* + *cfd* (= centrale tibiale distale plus centrale fibulare distale).

The *t* = tibiale is formed as an element of no small size on the plantar side between the navicular and the talus.

The *ph* = prehallux is formed only in mesenchyma.

Cavia cobaya:

Petri 1935 found the following independent elements in 8 embryos:



. = plantar sesamoid bones
 Mem: note the proximo-tibio-plantar one at the base of mtV.

The 5th metatarsal is rudimentary.

The 1st metatarsal is found — but as a rudiment — only in the youngest embryo (ab. 20 days old). In older embryos it has entirely disappeared.

E. EDENTATA (EDENTATES).

Baur 1886 (*tatusia hybrida* — *tatusia novemcinctus* — *choloe-
pus didactylus* — *manis brevicaudatus*).

Weber 1891 (*manis tricuspis*).

Ursing 1932 (*bradypus tridactylus*).

Schmidt-Ehrenberg 1942 (*dasypus hybridus* Desm.).

Manis tricuspis:

Weber 1891 found the following independent elements:

T	F
	a ca
	nav
x	cub
t_1 t_2 t_3	
I II III	IV V
2 3 3	3 3

x is an extra bone articulating with the navicular, found also in adults.

Bradypus tridactylus:

Ursing 1932 found the following independent elements:

T	F	(adult)	T	F
	a		a	ca
t				
$c_1 = c_2$				
	cub			cub
t_1 t_2 t_3			nav	
I II III	IV V		t_1 t_2 t_3	
1 3 3 3 1			I=II=III IV=V	
			3 3 3	

The astragalus consists of 1 element only, which *Ursing* explains as *i* = intermedium. But after comparative investigations the possibility seems to suggest itself that a *cpr* = centrale proximale may be concealed in this bone.

Calcaneum: In addition to a main prochondral centre there are found several small ones, *viz.* a disto-dorsal (not later

identifiable, however), a disto-tibio-plantar (identified as sustentaculum), and several uncertain centres. This gives *Ursing* occasion to remark that differentiation from mesenchymal tissue to prochondral cartilage may begin in several places.

The navicular is developed from 3 elements, a large dorsal centre (c_1 = centrale 1), a small tibio-plantar centre (t = tibi-ale), and a small dorso-fibular centre (c_2 = centrale 2).

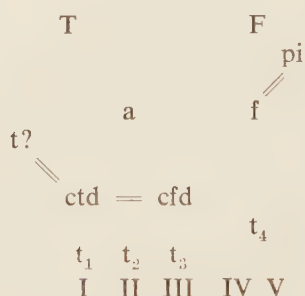
The cuboid is formed of 1 element only (*Ursing* does not at all mention t_5 = tarsale distale 5).

The 1st and 5th metatarsals are rudimentary.

At later stages the distal tarsal bones unite with each other and with the metatarsals. The united areas may vary somewhat for the different animals. The lines of division between the individual bones are always easily discernible.

Dasypus hybridus Desm.:

Schmidt-Ehrenberg 1942 found the following independent elements:



The astragalus is formed of 1 element only (must be supposed to consist of $i \perp ctp$ (= intermedium plus centrale tibiale proximale). cfp = centrale fibulare proximale is not developed.

The navicular is formed of 2 equally large elements situated side by side, viz. $ctd \mid cfd$ (= centrale tibiale distale plus centrale fibulare distale). At later stages there is found a proximally directed process on the tibial side of the navicular. This process may correspond to t = tibi-ale.

The t_4 = tarsale distale 4 is connected only with the 4th metatarsal; but secondarily also with the 5th metatarsal. Nothing is stated about t_5 = tarsale distale 5.

The 1st and 5th metatarsals are rudimentary.

F. CARNIVORA (CARNIVOROUS ANIMALS).

Retterer 1884 (felis catus — canis fam.).

Baur 1886 (felis catus — canis fam. — mustela vulgaris — putorius ermineus — lutra).

Carlsson 1890—1891 (ursus arctos).

Schmidt-Ehrenberg 1942 (felis catus L.).

Ursus arctos:

Carlsson 1890—1891 found in 1 embryo a tibial marginal bone corresponding to os tibiale. Otherwise no further information.

G. PROBOSCIDEA (ELEPHANTS).

Baur 1886 (no special animals mentioned).

Bardeleben 1894 (elephas Africanus).

Fischer 1903 (hyrax Syriacus).

Ursing 1934 (procavia daemon).

Hyrax Syriacus:

Fischer 1903 found the following independent elements:

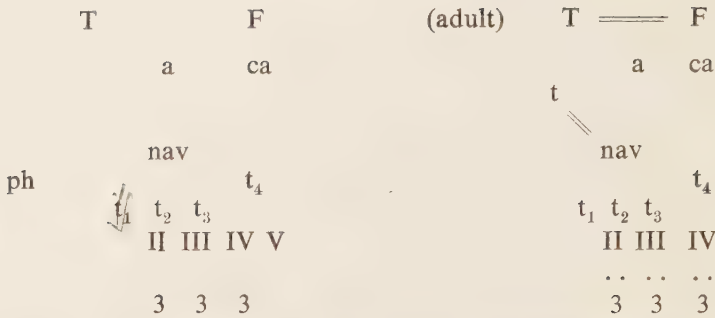
T		F		(adult)	
	a	ca		a	ca
				//	
t				t	
	nav			nav	
ph		cub			cub
	t ₁ t ₂ t ₃			(t ₁) t ₂ = t ₃	
	II III IV V			II III IV	

ph = prehallux, *t*₁ = tarsale distale 1, and 5th metatarsal are rudimentary in embryos, while in adults only a small rudimentary *t*₁ = tarsale distale 1 is left.

No demonstrable division of astragalus, calcaneum, navicular, or cuboid. As regards the astragalus he specially remarked that he had not succeeded in finding any element that might correspond to *Bardeleben's* intermedium tarsi.

Procavia daemon:

Ursing 1934 found the following independent elements:



The t = tibiale is not found as an independent formation. In adults a proximally directed process may be found plantotibially on the navicular. This is supposed by *Ursing* to be the t , a view which is supported by the fact that in one case he found an independent ossification centre in it (it was connected with the navicular by hyaline cartilage).

The astragalus is constricted in the middle. It must contain an i = intermedium, but *Ursing* does not pronounce further on this bone. Also the calcaneum is constricted in the middle, but he does not pronounce further on this bone either.

The ph = prehallux is present as an independent element in the embryo, but not so in the adult animal (here he states, however, that in the same area there is found a rudimentary t_1 = tarsale distale 1. He gives no information as to why he calls it ph = prehallux in one place and t_1 = tarsale distale 1 in another).

t_2 = tarsale distale 2, t_3 = tarsale distale 3, and t_4 = tarsale distale 4 are connected with the corresponding metatarsal bones by condensed mesenchymal tissue.

The 5th metatarsal is rudimentary, and has disappeared in adult animals.

H. UNGULATA (UNGULATE QUADRUPEDS).

Artiodactyla (with paired toes):

Retterer 1884 (bos — ovis — sus).

Baur 1886 (bos — ovis — camelus — lama vicugna — cervus capreolus — sus).

Schmalhausen 1908 (sus scropha dom.).

Suschkina-Popowa 1915 (bos — sus).

Carlens 1927 (bos).

Schmidt-Ehrenberg 1942: (bos taurus L. — sus scropha dom. L.).

Perissodactyla (with non-paired toes):

Retterer 1884 }
Saarni 1921 } equus.
Carlens 1927 }

Baur 1886 (no special animals mentioned).

Bos spec.:

Suschkina-Popowa 1915 and *Carlens* 1927 found the following independent elements:

T		F	(adult)	T	(F)
	a	ca		a	ca
	nav			nav	
		cub			cub
t ₁	t ₂	t ₃		t ₁	t ₂ =t ₃
(I)	II	III IV V			II=III-IV=V
	1	3 3 1			3 3

Suschkina-Popowa indicates that the cuboid is differentiated from a primordium common with the 4th metatarsal (states nothing of t_5 = tarsale distale 5). The astragalus must correspond to i = intermedium; t = tibiale is not formed; t_1 = tarsale distale 1, as well as 2nd and 5th metatarsals are rudimentary. The 1st metatarsal is found only at the earliest stages, and here only as a condensed mesenchymal substance.

The fibula is rudimentary in the adult animal. Distally it is found as an independent bone: os malleolare.

Carlens states that there are found paired sesamoid and metatarsophalangeal bones, and a few interphalangeal bones.

Sus spec.:

Schmalhausen 1908 found the following independent elements:

T		F
	a	ca
	nav	cd ₃
		cub
t ₁	t ₂	t ₃
	II	III IV V

The astragalus is probably formed of $i + cpr$ (= intermedium plus centrale proximale).

The cuboid is probably formed of $t_4 + t_5$ (= tarsale distale 4 plus tarsale distale 5). Later cd_3 = centrale distale 3 fuses with these two elements. (In the rat the cd_3 fuses to the navicular).

The navicular is probably formed of cd_2 = centrale distale 2 (theoretically it is possible that also the cd_1 = centrale distale 1 is included).

2nd and 5th metatarsals are rudimentary.

The t = tibiale is not laid down.

Sus spec.:

Suschkina-Popowa 1915 found the following independent elements:

T			F		
a			ca		
nav			cub		
t_1	t_2	t_3			
(I)	II	III	IV	V	
	3	3	3	3	

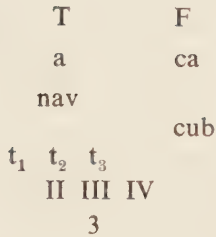
The t = tibiale is not laid down.

The 5th metatarsal is only secondarily connected with the cuboid. The 1st metatarsal is found only at the earliest stages and only as a condensed mesenchymal substance. The 2nd and 5th metatarsals are rudimentary, and so are also the corresponding phalanges.

Both *Schmalhausen* and *Suschkina-Popowa* show that the tarsale is laid down in one with the corresponding metatarsal. The tarsale is not differentiated out till a later stage.

Equus s. str.:

Saarni 1921 and *Carlens* 1927 found the following independent elements:



t_1 = tarsale distale 1 and t_2 = tarsale distale 2 fuse at an early stage. The 2nd and 4th metatarsals are rudimentary.

J. CHIROPTERA (BATS).

Baur 1886 (no special animals mentioned).

Schmidt-Ehrenberg 1942 (molossus spec.).

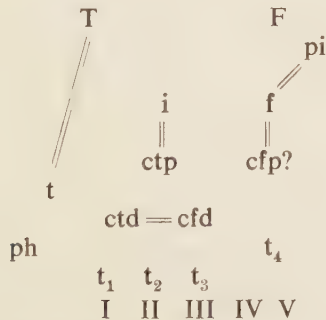
K. INSECTIVORA (INSECTIVORES).

Baur 1886 (erinaceus europaeus — talpa europaea — sorex vulgaris — centetes ecaudatus — scalops argentatus — scalops aquaticus — condylura cristata — blarina brevicaudata).

Schmidt-Ehrenberg 1942 (hemisentetes semispinosus Cuv. — erinaceus europaeus L. — leucodon araneus L.).

Hemisentetes semispinosus Cuv.:

Schmidt-Ehrenberg 1942 found the following independent elements:



t = tibiale is barely visible tibially in the tip of the tibial malleolus. Distal to t the ph = prehallux is seen as a mesenchyma condensation.

f = fibulare: pi = pisiformis is plainly recognizable proximally in this element. Possibly f contains distally cfp = cen-

trale fibulare proximale. The calcaneum is thus supposed to be formed of 3 elements.

$i + ctp$ (= intermedium plus centrale tibiale proximale) constitute one bone (astragalus), which is supposed to have developed from the two above elements.

$ctd + cfd$ (= centrale tibiale distale plus centrale fibulare distale) have likewise fused (navicular), but each element is plainly discernible.

t_4 = tarsale distale 4 is exceedingly big. Only one element is distinguishable. It articulates both with the 4th metatarsal and with the 5th metatarsal.

L. MARSUPIALIA (MARSUPIALS).

Baur 1885 and 1886 (early pouch stages of: *didelphys virginiana* — *didelphys murina* — *didelphys quica* — *halmaturus spec.* — *dasyurus viverrinus* — *phalangista Cookii* — *phascolarctos cinereus*).

Emery 1894—1897 (*phascolarctos cinereus* — *aepyprymnus rufescens*).

Schmidt-Ehrenberg 1942 (11 mm. long pouch stage of *didelphis marsupialis* L.).

Aepyprymnus rufescens:

Emery 1894—1897 found the following independent elements:

	T			F	
	ta			ca	
t					
	c ₁	c ₂			
				t ₄	t ₅
	t ₁	t ₂	t ₃		
	I	II	III	IV	V

The talus is analogized with i = intermedium.

t = tibiale is not found as an independent element at later stages, whether this is because it disappears or because it fuses with the elements forming the tibial malleolus.

c_1 = centrale 1 and c_2 = centrale 2 fuse to form the navicular.

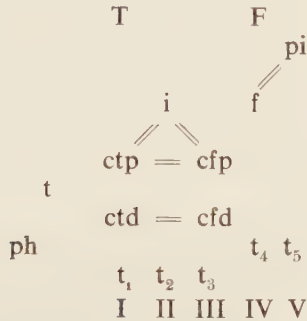
t_1 = tarsale distale 1 and the 1st metatarsal are rudimentary.

Having found both independent t_4 = tarsale distale 4 and t_5 = tarsale distale 5 *Emery* concluded that the future cuboid is formed by fusion of these two elements.

Finally he mentions a cartilaginous element found plantar to the base of the 4th metatarsal and corresponding to the plantar bone present in adults.

Didelphis marsupialis L.:

Schmidt-Ehrenberg 1942 found the following independent elements:



i = intermedium, *ctp* = centrale tibiale proximale, and *cfp* = centrale fibulare proximale lie close together, but the 3 elements are nevertheless distinct. *i* forms the body, *ctp* and *cfp* the head of the astragalus.

ctd = centrale tibiale distale and *cfd* = centrale fibulare distale lie close together (forming the navicular), but the 2 adjacent equally large elements are distinct.

f = fibulare and *pi* = pisiforme lie close together, but the 2 elements are distinct. *f* forms the anterior bigger portion of the calcaneum and *pi* the posterior.

*t*₄ = tarsale distale 4 is strikingly large. It articulates with the 4th metatarsal as well as with the greater part of the 5th metatarsal. Only the fibular corner of the 5th metatarsal articulates with the small rudimentary *t*₅ = tarsale distale 5. She does not know whether *t*₅ = tarsale distale 5 is later resorbed or fuses to *t*₄, but she is inclined to think that it is resorbed.

t = tibiale and *ph* = prehallux are not found as cartilaginous elements, but as dark nests of cells.

M. MONOTREMATA

Baur 1886 (ornithorynchus).

Emery 1897—1901 (echidna hystrix).

Echidna hystrix:

Emery 1897—1901 found the following elements:

T		F
	ta	ca
t		
	nav	
		cub
t ₁ t ₂ t ₃		
I II III		IV V

Emery could find only one primordium for each of the elements.

II. BIRDS

The embryonic foot of the bird is constructed on a line with those of other vertebrates, although it is seen in the full-grown bird to have undergone a development of its own. Two investigators will be mentioned here:

Holmgren 1933 (*larus canus* — *ploceus*).

Lutz 1942 (*dromiceius novaehollandiae* — *anas boscas* var. *domesticus* — *gallus bankiva* var. *domesticus*).

Dromiceius novaehollandiae:

Lutz 1942 found the following independent elements:

	T		F
			pi
		i	f
		ctp	cfp
t			
		ctd	cf
ph			d
	t ₁ t ₂ t ₃ t ₄ t ₅		
	I II III IV V		

t₁ tarsale distale 1 and t₅ = tarsale distale 5 are rudimentary. At a later stage they disappear entirely, while at the same time there occurs fusion of t₂ = tarsale distale 2, t₃ = tarsale distale 3, and t₄ = tarsale distale 4.

The 1st and 5th metatarsals are rudimentary, notably the 1st; they do not entirely disappear, however.

cfp + *cf d* (= centrale fibulare proximale plus centrale fibulare distale) are present in the form of a tissue thickening, which must be explained as fused *cf* = centralia fibularia.

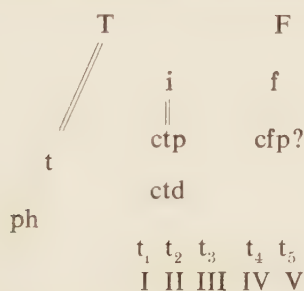
t + *ph* (= tibiale plus prehallux) are found as a pointed tissue thickening proceeding from the distotibial corner of *T* = tibia. Disappears later.

ctp + *ct d* (= centrale tibiale proximale plus centrale tibiale distale) lie as an independent formation. Microscopy reveals this formation to be constructed of 2 equally large elements. *ctp* must be supposed to contain a rudimentary *i* = intermedium, since a process is found proximally between *T* = tibia and *F* = fibula.

pi = pisiforme is supposed to disappear at later stages.

Anas boschas var. domestica:

Lutz 1942 found the following independent elements:



*t*₁ = tarsale distale 1 and *t*₅ = tarsale distale 5 are rudimentary, but do not entirely disappear. *t*₂ = tarsale distale 2, *t*₃ = tarsale distale 3, and *t*₄ = tarsale distale 4 fuse at a later stage. *ctp* = centrale tibiale proximale and *ct d* = centrale tibiale distale are distinct, but fuse at a later stage. A process consisting of connective tissue proceeds from *ctp* proximally between *T* = tibia and *F* = fibula. This process is explained as a greatly reduced *i* = intermedium.

cfp = centrale fibulare proximale and *cf d* = centrale fibulare distale are not definitely present. The former is perhaps visible, but disappears again later.

t + *ph* (= tibiale plus prehallux) are present as a pointed tissue thickening proceeding from the distotibial corner of *T* = tibia.

pi = pisiforme is not developed.

The 1st and the 5th metatarsals are rudimentary, particularly so the 5th.

III. REPTILES

The feet of these animals show greater accordance with those of mammals. Among the writers who have undertaken histological investigations the following will be mentioned here:

Gegenbaur 1864 (*Iacerta muralis*).

Sewertzoff 1908 (*Ascalabotes fascicularis* — *emys lutaria* — *seps chaloides*).

Rabl 1910 (*Chelonia mydas* — *emys lutaria* — *testudo graeca* — *crocodilus biporcatus* — *crocodilus niloticus* — *caiman latirostris* — *hatteria*).

Holmgren 1933 (*Agama colonorum* — *Chrysemys marginata* — *crocodilus niloticus* — *Sternothaerus*).

Steiner 1934 (*caiman crocodilus*).

Ascalabotes fascicularis:

Sewertzoff 1908 found the following independent elements:

T		F		(adult)	T	F			
	a		f			a=====f			
	c					c			
x					x				
t ₁	t ₂	t ₃	t ₄	t ₅ ?	t ₁	t ₂	t ₃	t ₄	
I	II	III	IV	V	I	II	III	IV	V
2	2	3	4	3	3	3	4	5	4

The tarsal bones and the corresponding metatarsals are differentiated from a common primum, thus t_4 = tarsale distale 4 from the 4th metatarsal, and even at a point of time when the 4th metatarsal is completely separated from the 5th ray. Accordingly t_1 cannot contain t_5 = tarsale distale 5. At a later stage the 5th ray unites with t_4 . t_5 must, therefore, be supposed to lie concealed basally in the 5th metatarsal, from where it is not differentiated.

c develops as a process on a = astragalus and somewhat later than *a*. There can be no doubt that *c* is a centrale.

x is the meniscus Born. There is some doubt as to what this actually means.

Seps chalcides:

Sewertzoff 1908 found the following independent elements:

T	F				(adult)	T	F			
	a		f				a=====f			
		t ₃	t ₄					t ₃	t ₄	
	II	III	IV	V				II	III	IV V
								2	3	3

a = astragalus possibly contains a centrale.

The 2nd metatarsal possibly comprises t_2 = tarsale distale 2.
The 1st metatarsal is not developed.

Emys lutaria:

Sewertzoff 1908 found the following independent elements:

T	F				(adult)	T	F			
	a		f				a=====f			
	c ₁ = c ₂						c ₁ = c ₂			
t ₁	t ₂	t ₃	t ₄			t ₁	t ₂	t ₃	t ₄	
I	II	III	IV V			I	II	III	IV V	

There seem to be two centralia. They have connection with a = astragalus, in such a manner that c_1 = centrale 1 is the connecting link.

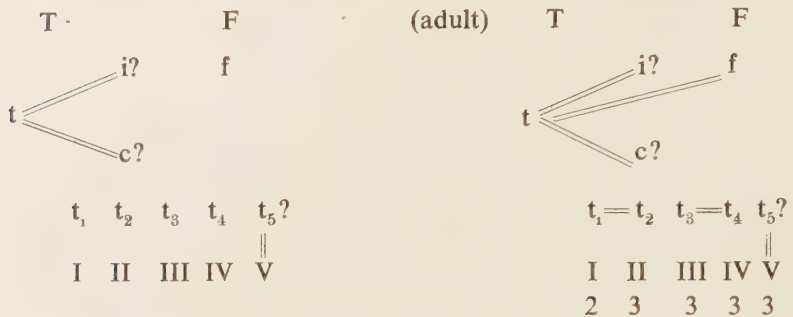
Sewertzoff indicates, as a feature common to reptiles, that tarsal bones, metatarsals, and phalanges develop from a common undivided prochondral primordium. Secondarily first the tarsal bones, then the metatarsals, and finally the different phalanges are differentiated from this common element. The t_5 = tarsale distale 5 has never been observed as an independent formation in any reptile, neither embryologically nor anatomically in adult animals.

The element a , as Sewertzoff chooses to call it (astragalus), is generally by others called tibiale or tritibiale. The reason why he does not approve of these names, but prefers the neutral astragalus is that they suggest the genesis, though this is uncertain. He himself is of the opinion — after comparative investigations — that the bone must have developed from $i + t$

(= intermedium plus tibiale), but he has never been able to prove this hypothesis embryologically.

Chelonia mydas:

Rabl 1910 found the following independent elements:

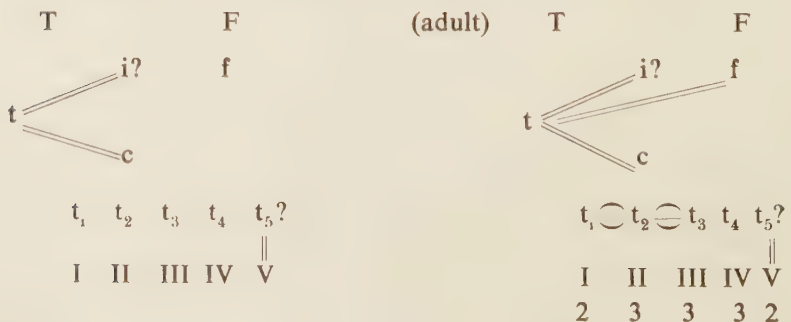


Rabl supposes the element tritibiale to have developed by fusion of $i + t + c$ (= intermedium plus tibiale plus centrale), although he has seen only 1 independent element.

There are found only the four tibial tarsalia distalia, each with a corresponding metatarsal. t_4 = tarsale distale 4 is thus primarily connected only with the 4th metatarsal. At a later stage it is seen how the 5th metatarsal gradually comes into contact with t_4 , as is the case in adult animals. This goes definitely against the hypothesis that t_4 should have been formed of $t_4 + t_5$. t_5 = tarsale distale 5 has not been found as an independent element. *Rabl* believes it to form part of the base of the 5th metatarsal.

Emys lutaria:

Rabl 1910 found the following independent elements:

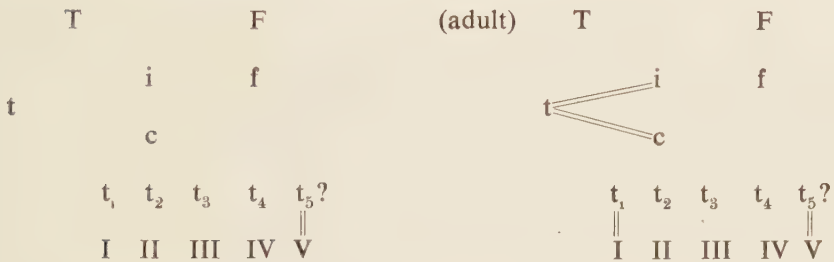


The conditions are exactly the same as in the case of *chelonias mydas*; only there seems here to be no doubt that the tritibiale consists of at least 2 elements, $i + t$ (= intermedium plus tibiale) and c = centrale. Yet he has not found complete separation between these 2 elements.

In adult animals the four distal tarsal bones may be independent, or there may have occurred fusion either between t_1 = tarsale distale 1 and t_2 = tarsale distale 2 or between t_2 = tarsale distale 2 and t_3 = tarsale distale 3.

Crocodilus:

Rabl 1910 found the following independent elements:



There is here no doubt that the future tritibiale has developed by fusion of 3 independent elements (i = intermedium, t = tibiale, and c = centrale).

t_1 = tarsale distale 1 is rudimentary and fuses at a later stage to the 1st metatarsal.

As for t_4 = tarsale distale 4, t_5 = tarsale distale 5, and V = 5th metatarsal the development is the same as in *chelonias mydas*.

Rabl, after examination of embryos of turtle, crocodile, and New Zealand lizard, emphasizes that he has found no evidence to suggest that $t_5 + V$ (= tarsale distale 5 plus 5th metatarsal) should be laid down as 2 independent elements. That nevertheless he believes this to be the case, though others hold that t_5 has fused with t_4 , is due to the fact that through his embryological investigations he has found that primarily t_4 is connected only with IV , and that the element of $t_5 + V$ does not get into contact with t_4 till a later stage. Furthermore none of the embryological preparations have revealed even the slightest signs of development of t_4 by fusion of t_4 and t_5 .

Crocodilus niloticus:

Holmgren 1933 found the following independent elements:

T	F	(adult)	T	F
	pm			pm
i	f		i	f
c ₁			c ₁	
t			t	
c ₂ c ₃ c ₄			c ₂ =c ₃ =c ₄	
t ₁ t ₂ t ₃ t ₄			t ₁ t ₂ =t ₃ t ₄	
I II III IV V			I II III IV V	

$i + c_1$ (= intermedium plus centrale 1) are laid down in one, but 2 equally large elements are easily distinguishable. c_2 = centrale 2, c_3 = centrale 3, and c_4 = centrale 4 are not distinctly differentiated. They fuse to c_1 = centrale 1. t = tibiale fuses to c_1 at an early stage.

pm = postminimus fuses to f = fibulare at an early stage.

t_1 = tarsale distale 1 is differentiated, but is not particularly distinct. At a later stage it fuses to the 1st metatarsal.

The 5th ray is rudimentary. t_5 = tarsale distale 5 has not been demonstrated. It must be supposed to form part of the 5th metatarsal.

Caiman crocodilus:

Steiner 1934, by examination of 18 embryos, found the following independent elements:

T	F	(adult)	T	F
	pi			pi
i	f		i	f
ctp	cfp		cp	
t			t	
ctd	cf			
			cd	
t ₁ t ₂ t ₃ t ₄ t ₅			t ₁ t ₂ t ₃ t ₄ =t ₅	
I II III IV V			I II III IV V	

i = intermedium is large and is situated in close relationship to *ctp* = centrale tibiale proximale and to a rudimentary *t* = tibiale. The adult animal presents an os astragalo-naviculare, which is supposed to have developed by fusion of *i* + *cp* + *cd* + *t* (= intermedium plus centralia proximalia plus centralia distalia plus tibiale). *Steiner* found 2 ossification centres in this element.

The calcaneum is formed of *f* = fibulare. In adult animals the tuber must be supposed to have been formed of *pi* = pisi-forme, since the tuber has an independent ossification centre.

*t*₁ = tarsale distale 1 has probably fused to the 1st metatarsal in adults.

*t*₄ = tarsale distale 4 and *t*₅ = tarsale distale 5 must be supposed to have fused in adults.

IV. AMPHIBIANS

Various investigations have been made of the larvae of these animals. The following may be mentioned:

Anura (bufos):

Schmalhausen 1908 (pelobates fuscus — bombinator igneus — hyla arborea — rana temporaria — bufo variabilis).

Holmgren 1933 (pelobates fuscus — xenopus laevis — rana temporaria).

Urodela (hurodeles):

Gegenbaur 1864 (salamandra maculosa — triton).

Sewertzoff 1904, 1908 (siredon pisciformis — triton cristatus).

Schmalhausen 1910, 1917 (salamandrella kayserlingii — rani-dens sibiricus).

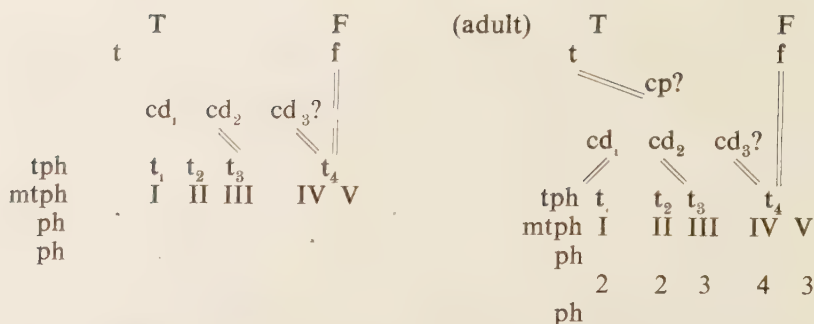
Steiner 1920—1921, 1922, 1934 (amblystoma tigrinum — cryptobranchus japonicus).

Holmgren 1933 (cryptobranchus — hynobius retardatus).

A few of these investigations will be reviewed.

Pelobates fuscus — bombinator igneus — hyla arborea —
rana temporaria — bufo variabilis:

Schmalhausen 1908 found the following independent elements:



Schmalhausen states that t_4 = tarsale distale 4 is formed from the distal end of f = fibulare. Moreover, he believes (but is unable to prove it) that there is found a cd_3 = centrale distale 3 (*Holmgren's* c_4) in t_4 = tarsale distale 4. The entire "calcaeus" should thus consist of $f + t_4 + cd_3$.

Further he believes that t_3 = tarsale distale 3 contains cd_2 = centrale distale 2 (*Holmgren's* c_3). In *rana* t_2 = tarsale distale 2 fuses to these elements at a later stage.

cd_1 = centrale distale 1 (*Holmgren's* c_2) and tph = tarsale prehallucis (*Holmgren's* cph = centrale prehallucis) fuse at later stages. In the bombinator alone the fusion occurs very early.

No t_1 = tarsale distale 1 is formed in *hyla* and *bufo*.

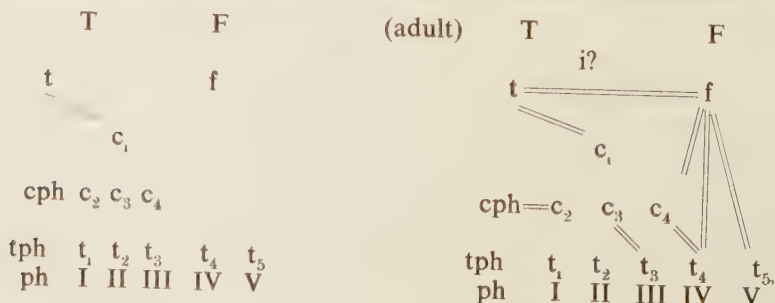
Schmalhausen emphasizes that there is found no i = intermedium. This element must have been lost in the course of the phylogenesis. The same is the case with t_5 = tarsale distale 5.

There are found no traces of cp = centrale proximale either (*Holmgren's* c_1). Such a fundamental element can hardly have disappeared, but must be supposed to form part of the t = tibiale.

Pelobatus fuscus — *xenopus laevis*

— *rana temporaria*:

Holmgren 1933 found the following independent elements:



t_4 = tarsale distale 4 and c_4 = centrale 4 fuse to f = fibulare. The same must be the case with t_5 = tarsale distale 5, at least in rana, where it is seen independent at first, soon to fuse to f = fibulare.

c_3 = centrale 3 fuses to t_3 = tarsale distale 3, and c_2 = centrale 2 fuses to cph = centrale prehallucis.

c_1 = centrale 1 actually forms the entire astragalus (previous writers thought c_1 to be t). A small process proximotibially on c_1 must be explained as t = tibiale.

i = intermedium is not seen, but it may be present in the connective cartilage proximally between c_1 = centrale 1 and f = fibulare.

Salamandrella kayserlingii:

Schmalhausen 1910 found the following independent elements:

	T			F	
			i		f
			cp		cf
t					
cd ₁		cd ₂	cd ₃		
tph	t ₁	t ₂	t ₃	t ₄	t ₅ tpm

cp = centrale proximale (*Holmgren's* c_1 [= centrale 1] = *Steiner's* ctp [= centrale tibiale proximale]) and cf = centrale fibulare (*Holmgren's* c_4 [= centrale 4] = *Steiner's* cfp [= centrale fibulare proximale]) fuse at later stages.

cd_1 = centrale distale 1 = *Holmgren's* cph (= centrale prehallucis) = *Steiner's* y (= centrale prehallucis).

cd_2 = centrale distale 2 = *Holmgren's* c_2 (= centrale 2) = *Steiner's* ctd (= centrale tibiale distale).

cd_3 = centrale distale 3 = *Holmgren's* c_3 (= centrale 3) = *Steiner's* cfd (= centrale fibulare distale), and

tpm = tarsale postminimus may remain independent or disappear.

t_5 = tarsale distale 5 manifests itself differently in different larvae. It may either remain independent or be more or less closely connected with t_4 = tarsale distale 4. In adult animals it seems always to be united with t_4 .

$t_1 + t_2$ (= tarsale distale 1 plus tarsale distale 2) is at the early stages seen to be constricted in the middle, a fact which shows that the formation must have developed from 2 elements.

The element called intermedium in adults must consist of $i + cp + cf$ (= intermedium plus centrale proximale plus centrale fibulare) (*Schmalhausen* does not expressly state so, but there can be no doubt about it).

Amblystoma tigrinum:

Steiner 1920—1921 found the following independent elements:

T						F						(adult)						T						F					

Chapter 4.

DISCUSSION ON GENESIS OF ACCESSORY BONES

I. *Discussion I: Accessory Bones Preformed in Hyaline Cartilage (Phylogenetic, Neogenetic, and Anomalous)*

If the accessory bones develop from the independent hyaline cartilage elements, then my embryological material of 500 feet should — according to statistical calculations — present all the accessory bones occurring with a frequency higher than 1.18 per cent. Some one or other will perhaps insist that my material comprises only 250 feet, because the 500 are paired. This objection may to a certain extent be justifiable, at least where only bilaterally occurring accessory bones are concerned. If we hold to 250 feet the percentage figure is not 1.18, but 2.36.

The frequency figures indicated for the various accessory bones differ so much (see frequency Table pp. 20—21) that it is difficult to select the bones which can be said for certain to occur with a frequency exceeding 1.18 per cent, or 2.36 per cent respectively.

I have proceeded in the manner of including an accessory bone if only a single series of elaborate anatomical investigations of any size showed a frequency of the bone concerned exceeding 1.18 per cent (or 2.36 per cent). Where both anatomic and radiographic investigations were available I founded on the anatomic (the more so because in my case it was a radiographically doubtful bone). If finally only radiographic investigations were available I founded on the majority of these.

On this basis I ought to have found the following bones in my embryological material (no matter whether I use the percentage of 1.18 or that of 2.36):

calcaneus secundarius,
 os intermetatarsale I,
 os peroneum,
 os sesamoideum interphalangeale,
 os sesamoideum metatarsophalangeale,
 os sesamoideum partitum interphalangeale et metatarsophalangeale,
 os tibiale,
 os trigonum.

Of these accessory bones I find the following preformed in hyaline cartilage, with the percentage frequencies indicated for each bone:

os intermetatarsale I: 6.8—8.0%,
 os peroneum: 0.4—0.4% (one pair of feet only),
 os sesamoideum interphalangeale dig. I: 56.0—57.8%,
 os sesamoideum interphalangeale proximale dig. V: 9.1—9.6%,
 os sesamoideum metatarsophalangeale II: 4.0—4.3%,
 os sesamoideum metatarsophalangeale III: 0.5—1.1%,
 os sesamoideum metatarsophalangeale IV: 2.7—2.7%,
 os sesamoideum metatarsophalangeale V: 26.2—26.2%,
 os sesamoideum partitum interphalangeale dig. I: 1.8—2.7%,
 os tibiale: 6.4—7.6%.

In addition I find:

calcaneus accessorius: 0.6—0.8%,
 os cuneiforme I bipartitum: 2.4—2.4%,
 os interphalangeale: 1.9—2.7%,
 os paracuneiforme: 13.2—13.2%,
 os subfibulare: 0.2—0.4% (only once),

and others claim to have found:

os trigonum,
 os Vesalianum.

Of the remaining accessory bones my histo-embryological material can give no definite information, being too small — in proportion to the rarity of the bones — for conclusions to be drawn from it.

Can these independent cartilaginous elements be traced back to the primitive tetrapod foot, i. e. are they phylogenetic?

To be able to answer this question one must have a knowledge of the phylogeny and the ontogeny of the extremital bones.

A. THEORIES CONCERNING GENESIS AND DEVELOPMENT OF THE EXTREMITIES

It is not my intention in this place to discuss the different theories concerning the genesis of the extremities. Only there is reason just to mention the three theories acknowledged by different groups of investigators: the archipterygium theory, the ptychopterygium theory, and the "Schwielen"-theory. The "Schwielen"-theory being the least known it will be briefly sketched here.

The "Schwielen"-theory was first advanced by Böker 1927 on the basis of the maxims of the comparative biological morphology, which say that the evolution of an animal 1) depends on, 2) is characteristic of, and 3) is mutable with the climatic and geological changes in the world around. The primitive vertebrates developed within the Cambrian period, by different stages, from an originally unicellular creature.

The climatic and geological changes within the Silurian period altered the way of life of the primitive vertebrates, which, therefore, developed further into primitive extremity animals. These animals developed, through the influence of mechanical factors, first epithelial, and later also connective tissue thickening, the so-called "Schwielen", localized to the sites of the 4 future extremities. These are the first recognizable traces of extremities.

The primitive fish and the primitive land vertebrates were again developed from these primitive extremity vertebrates. In the course of the carboniferous and Permian periods a further development of the primitive land vertebrates took place, because of the altered conditions of life, into primitive amphibians, stegophalia, primitive reptiles, and primitive mammals.

Böker lets the following Table illustrate the development from one geological period to the next.

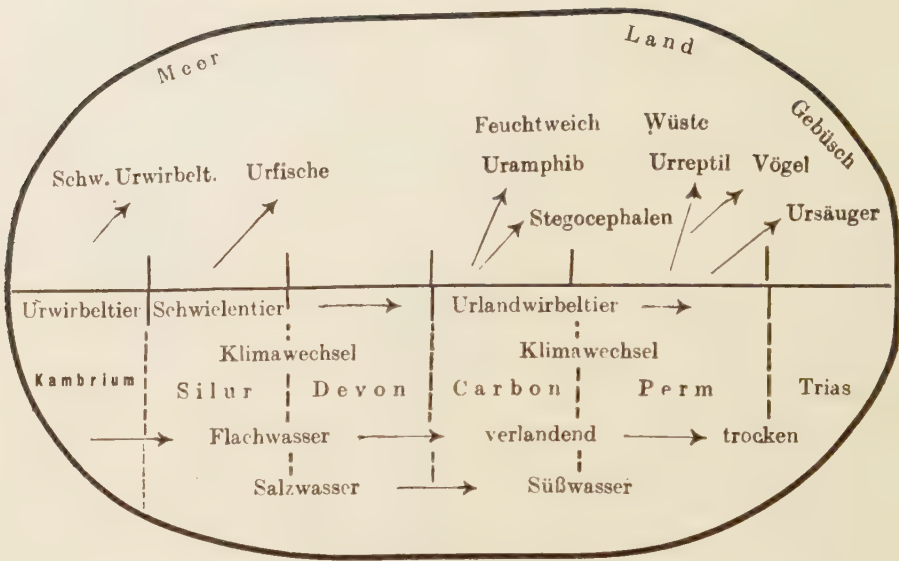


Fig. 119. (After Böker 1927). Development of vertebrates.

Böker's theory accords with that advanced by Sewertzoff 1931, who illustrates the conditions by the following diagram:

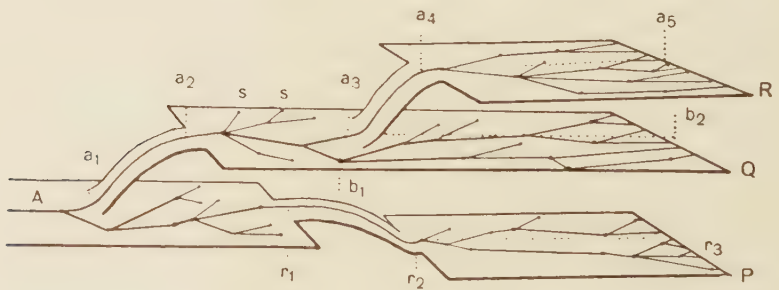


Fig. 120. (After Sewertzoff 1931). A random link in the evolution.

The diagram represents a single random link in the evolution, and the three planes P, Q, and R have stopped simultaneously in the evolution. It is seen how the descendants of the animal form A develop on different planes. Some are on a level with A, that is they are at the same evolutionary stage as A with regard to one or more properties, only they adapt themselves

more and more to the environments (*idio-adaptation*). Some descendants reach a higher level, that is the property or properties in question have developed to the profit of the animal (*aromorphosis*). Finally some descendants are at a lower level, which means that the property or properties concerned are under reduction (*degradation*).

If we take, for instance, an accessory bone, this means that a phylogenetic accessory bone can be traced back from a_5 by a_4 , a_3 , a_2 , and a_1 to the animal form A. Likewise, the same accessory bone, if present in b_2 , can be traced back by b_1 , a_2 , and a_1 . Finally, if it is not the accessory bone concerned that is under reduction it can also be traced from r_3 back to A by r_2 and r_1 .

If, on the other hand, the accessory bone is a link in the aromorphosis, it can be traced phylogenetically only to the aromorphosis concerned. Such an accessory bone I will call conditionally phylogenetic or, to avoid misunderstandings, *neogenetic* (neos = young, genos = birth). An accessory bone formed at a_4 can thus from a_5 be traced only to a_4 . One may examine any number of animals within b and on the whole within Q (and P) without ever succeeding in finding the accessory bone concerned.

It appears from the above statements that the phylogenetic origin of a bone becomes more and more certain the more often its presence can be demonstrated within animal orders and classes now alive. If, on the other hand, we find a certain bone in only one living animal order and its progenitors, this is by no means conclusive for the bone as a primitive foot element; on the contrary, the bone is most likely a neogenetic formation. The point is, in other words, to look for the features that are common to the different animal orders and classes and not the specific forms.

According among others to Schaffer 1930 and Sewertzoff 1931 the neogenetic bones are characterized also by being laid down at a later stage of the embryonic period than the phylogenetic. This accords with the theory that the properties conditioning the division of the animal world into types, classes, and orders are laid down earlier than those conditioning the division into families, genera, and species. However, Thilenius 1897 goes against this hypothesis, and even more definitely so

Nauck 1933, who refers to the fact that in mammals the carpus is laid down later than the metacarpus, whereas in lower animals the carpus has been found to be laid down earlier than the metacarpus. The carpus should then in some animals be younger and in others older than the metacarpus. This is hardly a tenable theory, however.

Nothing certain can be said as to how and when the aromorphosis arises, but it is reasonable to seek the answer to altered conditions of life in the aromorphosis. The aromorphosis does not occur suddenly, but takes place slowly, successively, and after the following plan. At a certain stage of the evolution it has proved expedient for an animal group to produce more resistant connective tissue in certain areas than that already present, because the tissues in these areas are exposed to increased mechanical strain (pressure, pull, minor commonplace traumas, etc.). Hence there occurs in each individual animal within its life time a gradual conversion of the existing tissue into different secondary connective tissue forms.

This leads us on to the question of primary connective tissue versus secondary connective tissue. This question will not be discussed further, but reference may be made to *Schaffer* 1903 and 1930, as well as *Weidenreich* 1923 and the literature reviewed by them. The conditions will here only just be briefly outlined.

The primary or phylogenetic connective tissue is formed in the indifferent mesenchymal tissue at an early stage of the ontogeny and in predetermined areas, the same in all vertebral species. The secondary or accessory or acquisite connective tissue develops postnatally in the individual animals in response to irritants acting from without. Its localisation depends, therefore, on the point of action of the irritant (*Schaffer* 1930).

The primary as well as the secondary connective tissue comprise different tissue forms (among others the chordoid connective tissue, as well as the chondroid, and the different cartilaginous tissues) without sharp lines of division between the different forms (*Schaffer* 1930). Generally it is impossible to demonstrate any histological differences between the primary and the secondary tissues. *Schaffer* holds, however, that such may be demonstrated in certain cases, a fact which has not yet been sufficiently investigated.

The different secondary connective tissues occur extensively in the entire animal world. It is characteristic of these tissues that the irritant acting from without may provoke different forms in parallel areas of different animals. Thus, for instance, the sesamoid nodules consist in sloths (*Bradypus* — *edentata* — mammals) of fatty tissue, in frogs (*Rana* — *Anura* — amphibians) and reptiles of chondroid tissue, which in many cases passes gradually into a cartilage-like tissue, and finally in man of cartilaginous and bony tissue (*Schaffer* 1930).

The secondary tissue produced by this time will next occur postembryonically through generations, dependent in the individual animals, on the mechanical strain.

Gradually the evolution will have reached the point where in an ever increasing number of cases these secondary tissues will be laid down independently of the mechanical strain. Finally the most important of the secondary tissues will be inherited. This means in the case of the bony tissue that they are preformed in hyaline cartilage, adopting the appearance of the primary tissue, only laid down somewhat later (*Schaffer* 1930). The aromorphosis is now finished. A neogenetic bone has developed. The fact that acquired expedient properties can be inherited has been demonstrated among others by *Stieve* 1924. Also deformities are often inherited, as is well-known.

B. CONSTRUCTION OF THE PRIMITIVE TETRAPOD FOOT AS COMPARED WITH THAT OF THE FOOT OF LIVING MAMMALS

It is necessary to know how the foot of the primitive land vertebrate, the so-called primitive tetrapod foot, is constructed, before one can decide whether the accessory bones are phylogenetic formations or not.

The investigations within this field being legion I shall confine myself to reporting the results of some of the recent elaborate works concerning these facts. For further details reference may be made to these works (and the literature mentioned there).

According to *Steiner* 1920—1921, 1922, 1934, 1935, and 1942, and his assistant *Schmidt-Ehrenberg* 1942, the primitive tetrapod foot is constructed as follows:

There is found a basal cord, in which femur — fibula — fibulare — tarsale 4 — metatarsale IV — 5 phalanges develop, and from which rays lead off on the tibial side:

1st ray leads off from the distal end of the femur and gives rise to: tibia — tibiale — prehallux.

2nd ray leads off from the distal end of the fibula and gives rise to: intermedium — centrale tibiale proximale — centrale tibiale distale — tarsale 1 — metatarsale I — 2 phalanges.

3rd ray leads off from the distal end of the fibulare and gives rise to: centrale fibulare proximale — centrale fibulare distale — tarsale 2 — metatarsale II — 3 phalanges.

4th ray leads off from tarsale 4 and gives rise to: tarsale 3 — metatarsale III — 4 phalanges.

In addition the following elements develop from the basal cord, but from the fibular side:

- 1) from the distal end of the fibulare: tarsale 5 — metatarsale V — 3 or 4 phalanges,
- 2) from the same place: postminimus,
- 3) from the distal end of the fibula: pisiforme.

Steiner does not mention the postminimus, but the pisiforme develops now from a point corresponding to the pisiform and now from one corresponding to the postminimus.

Diagrammatically the construction looks as follows:

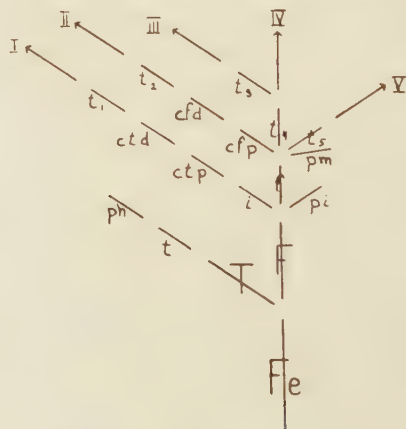


Fig. 121. Diagram showing the construction of the primitive tetrapod foot, drawn on the basis of *Steiner's* and *Schmidt-Ehrenberg's* statements.

Steiner and *Schmidt-Ehrenberg* conclude from their investigations that the foot of the living mammal has developed in the following manner from the elements of the primitive tetrapod foot.

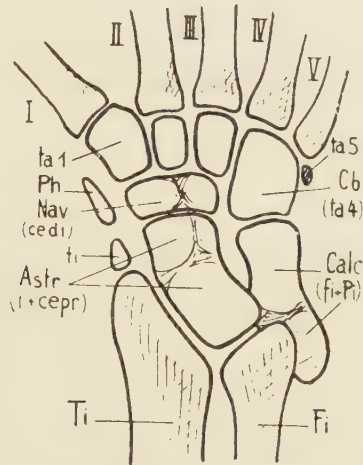


Fig. 122. (After *Steiner* 1942). The development of the foot of the living mammal from the elements of the primitive tetrapod foot.

According to *Holmgren* 1933 and 1939 the primitive tetrapod foot is constructed as follows:

We must distinguish between the stem and the rays.

The stem is constructed as follows: a tibial and a fibular portion branch out from the femur.

Tibia, tibiale, and centrale prehallucis develop from the tibial portion.

The fibula, after having developed into the fibular portion, is differentiated further into an intermediary and a fibular branch.

The intermediary branch develops into intermedium and centrale 1, after which the branch is divided further, forming centrale 2, centrale 3, and centrale 4.

The fibular branch develops into fibulare and pisiforme¹⁾.

The rays develop independently of the stem as tarsale pre-

¹⁾ *Holmgren* himself calls this element postminimus, but he states that it is homodynamic with the pisiform in the hand. As, however, *Schmidt-Ehrenberg* by postminimus and pisiform respectively understands 2 different elements in the foot, I prefer the term pisiform for the element

by *Holmgren* called postminimus, thus being in accordance with *Schmidt-Ehrenberg's* terminology.

hallucis, tarsale 1, tarsale 2, tarsale 3, tarsale 4, and tarsale 5, each with corresponding metatarsals and phalanges. *Holmgren* states nothing of the number of phalanges.

It should be remarked that a secondary fusion may take place, both between the different elements of the stem and between those of stem and rays.

The following Table illustrates the construction according to *Holmgren*.

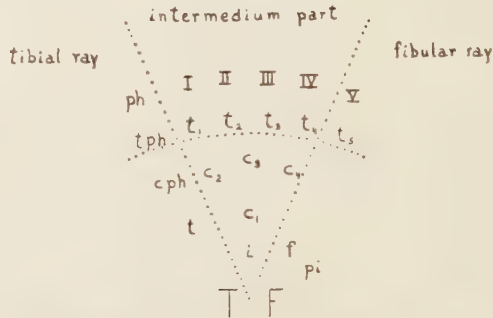


Fig. 123. Table showing the construction of the primitive tetrapod foot, set up on the basis of *Holmgren's* statements. It is worth noting that there is no main axis.

Holmgren concludes from his investigations that the foot of the living mammal has developed from the elements of the primitive tetrapod foot in the manner illustrated in Fig. 124.

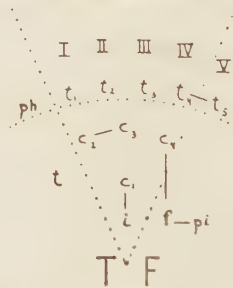


Fig. 124. (Mainly after *Holmgren* 1933). The development of the foot of the living mammal from the elements of the primitive tetrapod foot.

C. DETAILS OF THE GENESIS OF EACH INDIVIDUAL ACCESSORY BONE PREFORMED IN HYALINE CARTILAGE

After this survey of the primitive tetrapod foot and its development into the foot of the living mammal the accessory

bones preformed in hyaline cartilage will be dealt with individually.

1. *Os intermetatarsale I.*

According to the literature the intermetatarsium should occur only in the human foot. Yet, no definite conclusions can be drawn concerning the presence of this accessory bone in animals, because the number of systematic anatomic animal investigations is very small, and the accessory bones are generally not regarded as regular bones, so accordingly no particular attention is given to them.

Anatomically the intermetatarsium has not been found exclusively as an osseous formation, but also as a hyaline-cartilaginous element, e. g. by *Gruber* 1877 in young individuals, *Hasselwander* 1910 in a child aged 10, and *Tokmakoff* 1928—1929 in adults.

The literature contains no reports of an intermetatarsium found by histo-embryological examination, neither in man nor in animal. However, my findings (p. 68) leave no doubt that this bone is preformed in hyaline cartilage.

The intermetatarsium is thus an accessory bone preformed in hyaline cartilage, which apparently is found only in man. Hence it can hardly be phylogenetic, so accordingly it is not included in the diagrams indicating the development of the foot of the living mammal from the primitive tetrapod foot (*vide* p. 151, Fig. 122 and p. 152, Fig. 124). Besides, there is no element left from the primitive tetrapod foot to account for its existence.

Different explanations have been given in the literature concerning the intermetatarsium, thus for instance by the following investigators:

Gruber 1877 explains it as a formation preformed in hyaline cartilage. Furthermore, *Gruber* states that in the same place there is found a formation which is not preformed in hyaline cartilage, and which should not be regarded as an intermetatarsium. This latter formation has developed as an ossification in the tendon of origin of the interosseus dorsalis muscle.

Albrecht 1886 holds that the primitive tetrapod foot has 9 rays. He, therefore, explains the intermetatarsium as a metahallux.

Schwalbe 1917 explains the bone as a detached dorso-disto-

fibular corner of the tibial cuneiform. In addition he states that false intermetatarsea may be present, developed as ossifications in the tendon of origin of the interosseus dorsalis I accessorius.

Friedl 1924 explains the intermetatarseum partly as an ossification in the tendon of insertion of the interosseus dorsalis I, and partly as a failure of an independent ossification centre to fuse with the dorso-disto-fibular corner of the tibial cuneiform, from which it should form a process.

Tokmakoff 1928—1929, despite his hyaline cartilage finding, regards the bone as a mechanically developed ossification in the tendon of the interosseus I muscle.

Finally there is reason to mention that *Fischer* 1927 — unlike all other investigators — holds that in addition to the already mentioned elements in the primitive tetrapod hand (corresponding to the foot) there is found an ultimate series situated between the metacarpals, at the bases of the latter. He calls these elements *carpalia ultimalia*. *Fischer* claims to have demonstrated the presence of these elements in certain bufos, and he states that already *Baur* 1888 pictured them without further describing them, however. (I have not succeeded in procuring *Baur's* work).

Fischer has not seen these ultimate elements in the foot, but he believes to have found a tarsale ultimalia I in one of *Baur's* pictures from 1888 of an adult cryptobranchus maximus (urodele — amphibians). I dare not pronounce further on this finding.

In case *Fischer's* theory of the existence of ossa tarsalia ultimalia is correct, it should be possible to explain the intermetatarseum as such an element. So far, however, *Fischer* has been the only writer to advance this theory.

Therefore, I prefer for the present to regard the intermetatarseum preformed in hyaline cartilage as an anomaly characteristic of man (for anomalies, see under os cuneiforme I bipartitum p. 170). It is hardly a neogenetic bone, at least I can see no expediency in its presence.

2. *Os peroneum*.

Although I have found the os peroneum preformed in hyaline cartilage, the genesis of this bone will not be discussed further

in this place, for, as will be shown later (p. 201), my findings do not by any means justify me in regarding a hyaline cartilaginous primordium as the general cause of the presence of the os peroneum.

3. *Ossa sesamoidea metatarsophalangealia et interphalangealia.*

Apparently metatarsophalangeal and interphalangeal sesamoid bones may be observed within all living orders of mammals, and many of the inconstant bones in man are constant in animals. Observations of sesamoid bones have been reported even in extinct mammals. Thus *Thilenius* 1895 has shown that such were present in mammals within the triassic and eocenal periods.

Sesamoid bones preformed in hyaline cartilage have also histo-embryologically been found repeatedly in living mammals. These findings disprove, in the opinion of the writers concerned, the formerly held view that the sesamoid bones should be mechanically determined formations.

This unserviceableness of the mechanical theory was demonstrated in the first instance by *Pfitzner* 1892 through his comprehensive anatomic sesamoid bone investigations with consideration of sex, age, and profession, and by *Thilenius* 1896 through his histo-embryological investigations of the human hand.

Sesamoid bones are stated not to be present outside the class of mammals. I do not know whether this is actually the case, or whether the lacking observations of such bones are due to a failing interest in the question. Only once have I succeeded in finding in the literature a report of sesamoid bones preformed in hyaline cartilage observed outside the class of mammals. The finding was made by histo-embryological examination. It was a case of metacarpophalangeal formations in the ostrich (*Nassonov* 1896). These formations are, however, mentioned only in passing under the name of "cartilages accessoires".

Unlike sesamoid bones, sesamoid nodules are of very common occurrence within the different classes of vertebrates (including the mammals) (cf. *Schaffer* 1903 and 1930). Sesamoid nodules are small, indurated, well-defined thickenings consisting of compact, fibrous tissue, chondroid tissue, or tissue resembling

hyaline cartilage (*Pfitzner* 1892, *Retterer* 1884, *Retterer & Neuville* 1918, *Schaffer* 1930). The sites of these sesamoid nodules are the same as those of the sesamoid bones. A comparison between different mammals may even show that one species presents sesamoid nodules while another has sesamoid bones in the corresponding places. *Retterer* 1918 has even found both sesamoid bones and vesiculofibrous sesamoid nodules on the palmar side of the metacarpophalangeal joints of a man, aged 26 (vesiculofibrous sesamoid nodules were found also dorsally in these joints and in the interphalangeal joints. *Pfitzner* 1892 has once in man found a dorsal sesamoid bone in the 1st metacarpophalangeal joint). Accordingly there can hardly be any doubt that there exists an intimate relationship between sesamoid bones and sesamoid nodules, a relationship which strongly suggests that sesamoid bones (and nodules) belong to the secondary connective tissue (*vide* p. 148 and p. 205).

Sesamoid bones are never mentioned in descriptions of the primitive tetrapod foot (*vide* pp. 149—152). This may be due to the fact that they did not exist, but may also be due only to a failing interest in the question. The greatly varying pictures of and the interchanges between sesamoid bones and sesamoid nodules, as well as the presence of sesamoid bones chiefly, or even perhaps exclusively, in the mammals, add support to the view that sesamoid bones are neogenetic bones (a view already suggested by *Emery* 1894—1897). This means that they are bones preformed in hyaline cartilage which cannot be traced to the primitive tetrapod foot, but only a few steps towards it.

The purpose of the human sesamoid bone is not quite evident. It may have played its part and now be declining. At least only the 2 metatarsophalangeal bones of the big toe are constant, while many other mammals have constant sesamoid bones associated with all metatarsophalangeal joints.

4. *Ossa sesamoidea partita*.

Divided sesamoid bones have apparently been observed only in man. Regarding the conclusions that may be drawn from this fact reference may be made to the statements in the section dealing with the os intermetatarsale I (p. 153).

In the great majority of the cases the division is limited to the 2 constant sesamoid bones of the big toe. The investigations

reported below, therefore, all refer to these bones, where nothing else is indicated.

The division consists most often in a bipartition with a proximal and a distal segment, more rarely a tibial and a fibular. Only occasionally do we find division into three, four, or more segments. The first cases reported of division were those described anatomically by *Pfitzner* 1892. This writer found division of the tibial sesamoid bone in 2.1 per cent, of the fibular in 0.26 per cent, and partial division of the tibial or the fibular in 8.3 per cent. In subsequent statistical works based on radiographs the frequency figures varied a great deal (cf. frequency Table pp. 20—21). The highest percentage figure, i. e. 33.5 per cent, was obtained by *Kewenter* 1936 on the basis of radiographs from 3 different aspects.

The question of the genesis of the division has occupied many investigators, but no agreement seems to have been obtained as yet (except concerning the unquestionable cases of fracture¹). Therefore, only a few of the different opinions advanced will be briefly mentioned here (for further details reference may be made to *Boeminghaus* 1936, *Kewenter* 1936, and *Sundt* 1944).

Pfitzner 1892 can give no explanation to the occurrence of the division. *Schunke* 1901 regards it as a fracture. *Momburg* 1907 and *Igelstein* 1908 suggest the idea of congenital division, without reporting investigations in proof of, or even in support of such a theory. *Bizarro* 1921 assents without criticism to this view. *Renander* 1924, on the basis of elaborate histological investigations, suggests the possibility of an osteochondropathy similar to the aseptic bone necroses. *Müller* was in 1924 of the opinion that the division is due to the sesamoid bone being exposed to a continuous strain, which he has shown experimentally may lead to a linear cleavage of the bone, histologically resembling pseudarthrosis. However, in 1925 and 1927 *Müller* believes it to be an independent lesion with partial necrosis in a whole sesamoid bone. The division — reminiscent of a pseudarthrosis formation — should then be secondary and be

¹) According to *Kewenter* 1936 fracture is of rare occurrence. It is a diagnosis which should be made with great cautiousness. Definite proof of its presence is obtained only through 1) histological examination, 2) previous X-ray examination showing undivided sesamoid bone, or 3) demonstrable callus formation at follow-up examination.

due to the influence of mechanical factors on the diseased sesamoid bone.

Kimmerstiel, Kremser, & Richter 1933 regard the division as the result of minor traumas continually repeated, so that the injuries never get time to heal up. *Wisbrun* 1934 holds that the division arises by interaction of the following 3 pathological components: 1) development of 2 ossification centres, 2) delay of the ossification past the age of growth, and 3) a functionally or traumatically conditioned breaking of the continuity of the tissue situated between the 2 ossification centres. *Bennet* 1935 shows that the division may be due to an unspecific osteomyelitis.

Boeminghaus 1936 believes in an interaction of continually repeated minor traumas and 2 or more ossification centres. The intermediate cartilage constitutes a *locus minoris resistentia*. He shows how the intermediate cartilage degenerates and necroses; fissures develop, with subsequent ingrowth of unspecific connective tissue and vessels; and the necrotic tissue is resorbed. *Kewenter* 1936 shows that it is normal for sesamoid bones to have the ossification starting from different centres. The division must, in his opinion, be supposed to have connection with this fact, and must in the majority of the cases be regarded as non-pathological (it may also be pathological, however, e. g. be due to arthrosis deformans). *Sundt* 1944 regards the symptom-free division as a congenital anomaly. The cases giving rise to symptoms are in his opinion due to an attending aseptic bone necrosis, caused by continually recurring traumas.

Although numerous theories have been advanced as to the cause of the division, little attention has been paid to the question whether the hyaline cartilaginous primordia of the sesamoid bones may be divided. This possibility seems to have been mentioned only by *Hasselwander* 1903, 1910, and 1938, and *Boeminghaus* 1936. The former states that he has found no division in the cartilage stage by examination of sesamoid bones from 822 feet of individuals from before birth till 25 years of age, while the latter states that he has found no case of division among 134 tibial sesamoid bones from children between the ages of 0 and 12 years. The results of these investigations are not conclusive, however, being not derived from systematic, histological serial-section investigations.

Among the 404 feet (202 pairs) where the constant sesamoid bones are present my embryological serial-section analyses do not in a single case reveal division of the hyaline-cartilaginous primordium, not even the slightest suggestion of a division. It must, therefore, be justifiable to conclude, on the basis of the frequency of the division in adults and the size of my material, that a multinuclear hyaline-cartilaginous primordium is not generally the cause of the sesamoid bone division found in adults.

However, I succeeded only very occasionally in finding division of primordial sesamoid bones, i. e. the ossa sesamoidea interphalangealia hallucis (described p. 80). It must be permissible to conclude from these findings that sesamoid bone division in adults may in rare cases be due to a multinuclear hyaline-cartilaginous primordium.

Thus, the term congenital division has a certain justification, though, indeed, a very small one only. But the term ought never to be applied as a general expression for the cause of the sesamoid bone division. The best explanation to the sesamoid bone division in general seems, in my opinion, to be that suggested by *Boeminghaus*. The occurrence of a divided sesamoid bone should thus be an acquiste, postnatal phenomenon, and in rare cases perhaps a congenital anomaly (as for anomalies, see later under *os cuneiforme I bipartitum* p. 170).

5 and 6. *Os tibiale and os paracuneiforme.*

It seems natural to deal simultaneously with *os tibiale* and *os paracuneiforme*, because there is a certain parallelism between them, particularly as regards the question of a possible phylogenetic origin.

The *os tibiale* and the *os paracuneiforme* are of frequent occurrence, either as constant or as accessory bones, in the feet of full-grown living mammals and amphibians. They are found among others in the following animals:

Mammals.

Primates:

mycetes: *Bardleben* 1885,

hylobates: *Kohlbrügge* 1890—1891,

hapale: *Winge* 1893 (1941),
 cebus hypoleucus: *Monahan* 1920.

Prosimiae:

otolicnus crassicaudatus: *Carlsson* 1890—1891.

Rodentia:

According to the investigations made so far the os tibiale and the os paracuneiforme seem to have been found in practically all rodents (*Bardeleben* 1885, 1894, *Baur* 1885, *Bütschli* 1921, *Carlsson* 1890—1891, *Greene* 1935, *Howell* 1926, *Petri* 1935, *Pfitzner* 1892, *Spark & Dawson* 1928, *Tornier* 1891, *Winge* 1893 (1941), (*vide* further p. 120).

Edentata:

myrmecophaga: *Bardeleben* 1885, 1894, *Winge* 1893 (1941),
 dasypus sexcinctus: *Bardeleben* 1885, 1894,
 euphractes minutes: *Bardeleben* 1885, 1894, *Winge* 1893 (1941),
 manis: *Weber* 1891, *Winge* 1893 (1941),
 cycloturus: *Winge* 1893 (1941).

Pinnipedia:

arctocephalus cinereus: *Bardeleben* 1894,
 halichoerus grypus: *Carlsson* 1890—1891.

Carnivora:

lutra: *Bardeleben* 1885, 1894, *Pfitzner* 1887, 1892,
 canis familiaris: *Pfitzner* 1892,
 felis tigris: *Pfitzner* 1892,
 mustela: *Pfitzner* 1892,
 paradoxurus: *Bardeleben* 1885, 1894,
 hemigalea hardwickii: *Bardeleben* 1885, 1894,
 procyon: *Bardeleben* 1885, 1894,
 cercoleptes caudivolvulus: *Monahan* 1920, *Blainville* 1841,
 arctictis: *Blainville* 1841,
 nasua: *Blainville* 1841, *Bardeleben* 1885, 1894,
 viverra: *Blainville* 1841,
 ursus: *Blainville* 1841, *Pfitzner* 1887, 1892, *Winge* 1893 (1941),
 celurus fulgens: *Bardeleben* 1885, 1894,
 mephitis: *Bardeleben* 1885, 1894,
 corneptus mapurito: *Bardeleben* 1885, 1894,
 helictis orientalis: *Bardeleben* 1885, 1894,
 galactis (grisonia) vittata: *Bardeleben* 1885, 1894.

Proboscidea:

elephas: *Pfitzner* 1887,

hyrax *Syriacus*: *Baur* 1885, *Fischer* 1903.

Ungulata:

artiodactyla: 0.

perissodactyla: 0.

Chiroptera:

0.

Insectivora:

talpa: *Bardeleben* 1885, 1894, *Carlsson* 1890—1891, *Tornier* 1891, *Winge* 1893 (1941).

centetes: *Bardeleben* 1885, 1894,

hemicentetes: *Bardeleben* 1885, 1894,

ericulus: *Bardeleben* 1885, 1894,

myogale: *Bardeleben* 1885, 1894, *Winge* 1893 (1941),

urotrichus talpoides: *Bardeleben* 1885, 1894,

tupaja tama: *Bardeleben* 1885, 1894,

erinaceus: *Bardeleben* 1885, 1894, *Monahan* 1920, *Winge* 1893 (1941),

galeopithecus philipinensis: *Bardeleben* 1885, 1894, *Winge* 1893 (1941),

condilura cristata: *Tornier* 1891,

scalops aquaticus: *Tornier* 1891,

cladobates: *Winge* 1893 (1941),

sorex: *Winge* 1893 (1941).

Marsupialia:

trichosurus vulpecula: *Emery* 1894—1897,

didelphys: *Bardeleben* 1885, 1894, *Carlsson* 1890—1891, *Emery* 1894—1897, *Monahan* 1920, *Winge* 1893 (1941),

dasyurus hallicatus: *Emery* 1894—1897,

chironectes: *Bardeleben* 1885,

trichosurus vulpecula: *Emery* 1894—1897,

didelphys aurita: *Emery* 1894—1897,

dasyurus hallicatus: *Emery* 1894—1897,

didelphys virginiana: *Baur* 1885.

} pouch stages

Monotremata:

echidna: *Emery* 1897—1901, *Monahan* 1920,

Bardeleben 1885 pronounces only on monotremata in the general.

Amphibia:

Anura:

rana: *Bütschli* 1921, *Ecker & Wiedersheim* 1896, *Monahan* 1920, *Steiner* 1920—1921.

Urodela:

salamandra maculosa: *Bütschli* 1921,
ranadon Sibiricus: *Wiedersheim* 1876.

If the accessory bones found in man originate from the primitive tetrapod foot — of which the common occurrence among mammals and amphibians seems suggestive — they must belong to the tibial series of the primitive foot, according to the development of the foot of the living mammal from the elements of the primitive tetrapod foot.

To elucidate this question it is necessary to compare the histo-embryological investigations of numerous different vertebrates. Only then is it possible to see whether such elements belonging to the tibial series are really preformed in hyaline cartilage, and if they are, whether these hyaline-cartilaginous primordia persist as independent elements, disappear, or unite with the adjacent elements.

In connection with the solution of this question it is necessary also to decide as to the development of the navicular bone from the elements of the primitive tetrapod foot.

Os tibiale:

According to the development of the foot of the living mammal from the elements of the primitive tetrapod foot (pp. 149—152) the navicular must have developed from centrale tibiale distale (= centrale 2) and centrale fibulare distale (= centrale 3), in the manner that the centrale tibiale distale (= centrale 2) forms a smaller tibial portion. In the case of man *Schomburg* 1900 made observations, in the prochondral stage, which argued in favour of this hypothesis (*vide* p. 118). *Bardeleben* 1885 made similar observations (p. 116), but as constant elements, in 6 to 8 weeks old embryos. *Bardeleben* states that the elements found were cartilaginous. This must, however, be wrong, for according to both *Schomburg's* and own investigations (pp. 62—63) only the prochondral stage can have been reached at the points of time in question.

The histo-embryological investigations within the different animal classes (pp. 116—143) show that the tibiale may either remain independent or fuse with the primordial navicular. Is this also the case in man?

Bardeleben was the first to take up the question of navicular and tibiale on a histo-embryological basis. However, I do not agree with *Bardeleben* in his explanations, and, as no one else has tested *Bardeleben's* findings, I shall here enter further on the problems.

Bardeleben himself directly misinterpreted his finding by homologizing the tibial navicular element (which he supposes to form the tuberosity) found by him as a constant formation in human embryos with the constant 8th tarsal element (naviculare mediale = naviculare accessorium) observed in rodents. Furthermore he states that in adults he has sometimes found the tibial navicular element to be distinguishable from the rest of the bone by a definite line of junction, and sometimes he has found it as an isolated formation. As to this latter point *Bardeleben* changes his view some months later, now stating that only other writers have found the element as an isolated formation, whereas the small inconstant bones observed by himself on the inside of the tuberosity of the navicular have nothing to do with the above element, "es ist ein drittes Element, welches wohl als Sesambein oder Epiphyse oder dergleichen aufzufassen sein dürfte (?)".

However, I disagree with *Bardeleben* in his explanation. The constant tibial navicular element found by him in human embryos has, in my opinion, nothing to do with the 8th tarsal element seen in rodents. But *Bardeleben* showed that the human navicular develops from 2 elements. The same result is later arrived at for various animals (*vide* pp. 119—143), also rodents (*Holmgren* p. 121 and *Schmidt-Ehrenberg* p. 122). In rodents, however, an additional 3rd constant element is laid down — slightly proximo-tibial to the 2 others. This element, the naviculare mediale = naviculare accessorium, remains independent.

Thus, the writers are wrong who regard *Bardeleben's* findings as a proof that the os tibiale (externum) is an independent element preformed in hyaline cartilage.

Schomburg 1900, on the other hand, demonstrated the presence

both of a bipartite primordial navicular and a hyaline-cartilaginous primordium of the os tibiale (externum); but he was unable to further elucidate the facts, because he, too, had been captured by *Bardeleben's* misinterpretation. No other investigators seem either to have attached the proper importance to *Schomburg's* findings.

Finally *Francillon* 1933, through serial-section analyses of 21 human embryos (at the cartilage stage), has shown that there is found an inconstant os tibiale preformed in hyaline cartilage. He does not, however, venture on an interpretation of *Bardeleben's* and *Schomburg's* findings of a bipartite primordial navicular.

The presence of an inconstant hyaline-cartilaginous primordium of the os tibiale is demonstrated through own investigations, but in addition I have pointed out the fact that far more often than an independent os tibiale do we find a spur-shaped process, and that there is a continuous line of transition from no spur by spur to independent os tibiale (*vide* pp. 84—89).

My embryological findings correspond exactly to *Gruber's* 1871 and 1877 anatomical descriptions of the navicular. Fig. 125 shows *Gruber's* picture of the navicular .

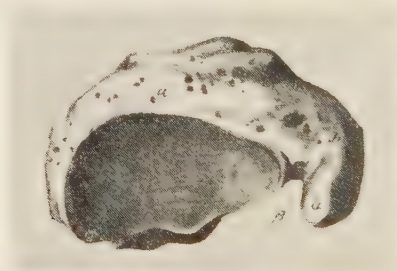


Fig. 125. (After *Gruber* 1871). Os naviculare.

According to *Gruber* the navicular has a more or less well-developed tuberosity on the planto-tibial side (b). This tuberosity is generally lined by a groove (β), sulcus navicularis, on the proximal side of the navicular. The tuberosity presents in 10 per cent of the cases a backwards directed process (processus tuberositatis navicularis - a), and in 2 per cent this process is developed maximally, being 10 to 15 mm. long. In 2 adults he has found the process as an independent bone (cf. my diagrammatic drawings Figs. 92—94, p. 88).

The embryological conditions in man may just be recapitulated: the navicular develops from 2 elements. In addition there may be found an inconstant 3rd element on the planto-tibio-proximal side, which may either remain independent or fuse to a smaller or greater extent with the tuberosity of the navicular.

By comparing these conditions with the histo-embryological findings in animals, and with our knowledge of the construction of the primitive tetrapod foot, we find that this 3rd element must be tibiale. Thus, the accessory bone: *os tibiale*¹⁾, observed in adult humans, can be traced back to the tibiale element of the primitive tetrapod foot and accordingly be accounted for on a phylogenetic basis.

(It is mentioned in the section dealing with coalescence that there is a possibility of accounting for the *os tibiale* on a phylogenetic basis even if it has not been preformed independently in hyaline cartilage. In the section dealing with secondary bone formations the possibility is discussed of explaining the *os tibiale* as such a formation).

Os paracuneiforme:

The *os paracuneiforme* seems — apart from my findings — never to have been found histo-embryologically in man. I find it in 13.2 per cent of my 500 feet, in other words, by no means infrequently.

This is the more surprising, because reports of its presence in the adult human foot are very rare. Personally I have found it only once, and even unilaterally in a boy, aged 13 (p. 34, Fig. 20).

This great difference in the case of man between the histo-embryological findings and the conditions in adults must be due to the fact that in the great majority of the cases the primordium disappears again, or at least does not undergo ossification.

According to the results of the comparative histo-embryo-

¹⁾ The *os tibiale* was by the end of the 19th century given the name *os tibiale externum*, because by that time the tibiale was thought to form the head of the talus. This is, however, wrong, according to our present knowledge; on the contrary it has been shown that the tibiale is the phylogenetic basis of the *os tibiale*. The addition of "externum" for this element is, therefore, only misleading and ought to be dropped.

logical and anatomical investigations of vertebrates the os paracuneiforme must be regarded as belonging to the tibial series within the primitive tetrapod foot, whether it be the centrale prehallucis or the tarsale prehallucis, or both.

Thus also the os paracuneiforme can be accounted for on a phylogenetic basis.

7 and 8. *Os subtibiale* and *os naviculare bipartitum*.

In connection with the above results with regard to the os tibiale and the os paracuneiforme there may be reason to give a brief account of the os subtibiale and the os naviculare bipartitum, 2 other accessory bones.

Os subtibiale:

Among full-grown vertebrates the os subtibiale has so far been found exclusively in adult humans.

The bone is found in a place where the presence of an element of the primitive tetrapod foot might be suspected. However, histo-embryological investigations have never revealed any element, neither in animal nor in man, which could be said for certain to underlie this bone. *Schmidt-Ehrenberg* 1942, however, makes suggestions in this direction, in so far as she states that in *microcebus myoxinus* (prosimiae — mammals) and *hemicentetes semispinosus* (insectivora — mammals) the tibiale is possibly found in close relationship to the tip of the tibial malleolus. Similar conditions have been suggested by *Lutz* 1942 for certain birds (*dromiceius novaehollandiae* and *anas boschas* var. *domestica*).

In the case of man no embryological observations have ever been made to justify such a conclusion. Here the tibiale always has a certain connection with the navicular. Thus, there is no definite basis for a phylogenetic origin of the os subtibiale.

Os naviculare bipartitum:

A bipartition of the navicular is a phenomenon which seems never to have been found in adult animals, but only in man.

A bipartition of the navicular can be explained phylogenetically on the basis of the histo-embryological animal investigations and the primitive tetrapod foot.

Such a proper phylogenetically explainable bipartition of the

navicular has, however, as far as I can see, never been described in the case of man. In such cases one should require, according to the histo-embryological findings, that the two portions are situated side by side, and are approximately equal in size (the fibular should be the larger), that together they form a normal navicular, and finally that the line of division is on a level with the middle of the tibial cuneiform (cf. also the facts concerning the os cuneiforme I bipartitum, p. 170).

None of the cases of os naviculare bipartitum reported in the literature fulfill these requirements. The navicular is in all these cases more or less deformed and the structure has generally partially changed, the fibular element being quite small and usually of a condensed structure. In the reported cases the occurrence of a bipartite navicular seems to have been due either to a pseudarthrosis of long standing, or to a division which has taken place in a primarily pathologically changed navicular (whether due to malacia [Müller 1927 and 1928, Weiss 1929], a statically transformed, rarefied or necrotic os naviculare [Simons 1930], sequelae of Köhler's disease [Wilke 1930], or pathological fracture in a necrotic os naviculare [Frosch 1931]).

9. *Calcaneus accessorius*.

The calcaneus accessorius is of rare occurrence in man, and it does not seem to have been mentioned in the cases of animals (as to the conclusions to be drawn from this fact, see p. 153 under the os intermetatarsale I).

Hasselwander 1910 as well as Holland 1928 and Francillon 1932 and 1934 regard the bone as developed by persistence of an independent ossification centre in the trochlear process of the calcaneum (cf. pp. 185-186 under inconstant ossification centres in calcaneum, and p. 195 under coalescence).

My investigations are the first to reveal the calcaneus accessorius as an element preformed in hyaline cartilage (*vide* pp. 65-66).

Since there is found no primitive tetrapod foot element corresponding to the site of the bone, and the bone has not been found embryologically in other vertebrates, my findings must be regarded as accidental anomalies (*vide* p. 170 under os cuneiforme I bipartitum).

10. *Os cuneiforme I bipartitum.*

According to *Gruber 1877* and *Böker & Müller 1936—1937* the bipartite tibial cuneiform is found exclusively in man. A review of the literature shows, however, that *Bardeleben* states in 1885 to have found slight traces of a bipartition in a possum (didelphys — marsupialia — mammals) and in 1894 to have found complete bipartition in a tree porcupine (*erethizon dorsatus* — rodentia — mammals). I have found no other similar observations reported in the literature, (as to the conclusions to be drawn, see p. 153 under *os intermetatarsale I*).

Histo-embryologically the following observations have been made, but only in man: *Bardeleben 1885* regards a bipartition as constant in the primordium; *Bardeen 1905* has in the prochondral stage found a fissure laterally in the primordial tibial cuneiform in 1 out of 6 cases. This fissure divides the primordium in a dorsal and a plantar portion; and *Schomburg 1900* has in ab. half of his cases found a divided tibial cuneiform in the prochondral stage (and simultaneously also a divided navicular), but the two segments fuse early in the cartilage stage. To these may be added my own observations (*vide pp. 66—68*).

Thus, we have to do here with an accessory bone preformed in hyaline cartilage, which apparently is of comparatively rare occurrence, having been demonstrated only once outside the human race, namely in a rodent. It appears from this fact and from the diagrams and Tables illustrating the development of the foot of the living mammal from the elements of the primitive tetrapod foot that the bone can hardly be of phylogenetic origin (*vide Figs. 122 and 124, p. 151 and p. 152*).

Gruber 1877 indicates two causes in theory of the existence of the bipartite tibial cuneiform, *viz.*: 1) 2 elements preformed in cartilage, and 2) occurrence of 2 ossification centres, which remain independent on account of failing fusion. Fracture, on the other hand, is in *Gruber's* opinion out of the question as cause.

Despite her diagram illustrating the development of the mammalian foot (p. 151) *Schmidt-Ehrenberg 1942* states, without having been able to prove it herself, that she accepts *Bardeleben's* explanation 1885 to the effect that the dorsal segment of the *os cuneiforme I bipartitum* should be regarded as the tar-

sale distale 1 and the plantar segment as tarsale distale prehallucis¹⁾ (*vide* p. 117). *Pfitzner* 1896 has likewise entertained the idea, without, however, believing in the correctness of this explanation. *Holtby* 1916, founding on *Pfitzner*, nevertheless writes quite categorically that "The significance of the condition is clear. The plantar segment corresponds to a rudiment of the seventh or tibial ray of the foot, or to the proximal portion of a prehallux".

It will be shown in the following that the conclusions mentioned above are mistaken. Since the 2 segments of the bipartite tibial cuneiform together constitute a normal tibial cuneiform, the human tibial cuneiform should, according to the above explanations, always develop from the 2 elements of the primitive tetrapod foot. This seems rather absurd, however, for why should the human tibial cuneiform be developed otherwise than those of animals? This is not the case either, as has been shown through my histo-embryological investigations, where I find partly a hyaline-cartilaginous paracuneiform (corresponding to the tarsale prehallucis) and at the same time a quite normal tibial cuneiform, and partly a paracuneiform concurrently with a bipartite tibial cuneiform.

Böker & Müller 1936—1937 express so to speak directly the opposite opinion with regard to the bipartite tibial cuneiform. While *Bardeleben*, *Holtby*, and *Schmidt-Ehrenberg* take it to be traceable to the beginning of time, *Böker & Müller* regard it as a phenomenon characteristic of the living human, which will occur with steadily increasing frequency, perhaps to become constant at a future time. *Böker & Müller* believe that the upright gait with the resulting greater charge on the tibial series makes the tibial cuneiform increase in size in the dorso-plantar direction, thereby reaching the plantar surface and thus contributing to a more even charge on the transverse arch of the foot. In this manner the tibial cuneiform becomes longer in the dorso-plantar direction than the other two cuneiforms, but, on the other hand, its size reduces the mobility of the transverse arch in the tibial direction. The enlarged tibial cuneiform must, therefore, aim at a horizontal longitudinal division, in order that the foot may regain sufficient elasticity.

¹⁾ In 1894 *Bardeleben* does not mention the prehallux in connection with the cuneiform, but writes only that the tarsale distale 1 corresponds to the os cuneiforme I dorsale and plantare.

As shown above, *Böker & Müller* are wrong in stating that the os cuneiforme I bipartitum is not found as independent dorsal and plantar primordia in embryos.

How to account for the os cuneiforme I bipartitum is not quite clear. Being preformed in hyaline cartilage, it may possibly be explained as a neogenetic accessory bone developed in man in consequence of the upright gait, (*Böker & Müller*). But then it is strange that it should be found also in a rodent, unless the bipartition is due here to a failing fusion of 2 ossification centres in an undivided hyaline-cartilaginous primordium. No investigations seem to have been made with the object of elucidating whether there may be found 2 such centres, but it is not impossible that there may, since this has been demonstrated in other animals (e. g. the dog, p. 189). Indeed, the objection might be raised in the case of the dog concerned that there was no proof that the 2 centres were found in an undivided hyaline-cartilaginous primordium.

On the other hand the bipartite tibial cuneiform may also be regarded as an accidental anomaly. It is impossible to give an exact definition of an anomaly, but in the general I regard as *anomalies* such ossicles or parts of ossicles which occur sporadically without known cause, and which have no influence on the shape or function of the foot. I distinguish between anomalies and deformities, without the lines of distinction being sharp, however. *Deformities* are generally easily perceptible, because they change the shape of the foot or affect its function (e. g. deformity of constant bones, absence of such bones, fusion, cleft foot, and the like). The anomalies may be reckoned among the accessory bones, but not so the deformities.

That exactly the same anomaly may occur time after time in both man and animal may at first seem extraordinary, but on reflection it is not so strange after all, for, as we all know the same deformities are often seen to occur in widely different animals (as pointed out among others by *Inhelder* 1904 and *Goldschmidt* 1910).

11. *Os interphalangeale.*

The os interphalangeale is a tiny bone, not much larger than a pin-head. In man it has, therefore, quite naturally been ascertained only radiographically, and even then extremely rarely.

According to the literature no description has been given of its occurrence in animal feet. This cannot, however, be regarded as a proof of its non-existence in animals.

Hasselwander 1910 has found the bone on the fibular side in the interphalangeal joint of the big toe, partly in a boy, aged 15, with open epiphyses, and partly in two individuals, aged 20 and 23 respectively, with closed epiphyses. Genetically he dares not leave out of account the possibility that it might be a rudiment of the medial phalanx of the big toe.

Schinz, Baensch, & Friedl 1939 have observed a similar case in a child, which, however, they explain as an intra-articular fracture. They do not state in which joint they have found the bone, but presumably it is neither big toe nor thumb.

It appears from my embryological investigations (p. 70) that the os interphalangeale occurs with a frequency of ab. 2 per cent, being, in other words, by no means so rare as the literature would justify one in thinking. (The lack of reports on this bone in the literature is probably among others due to the fact that the finding is of little interest).

Furthermore, it has been proved through my investigations that there is a close relationship between the os interphalangeale and a spur-shaped process from the base of the terminal phalanx of the big toe. In a few cases synchondrosis has even been seen to develop by the spur between the terminal and the proximal phalanges.

How to account genetically for the os interphalangeale, the spur, and the synchondrosis is not quite evident. *Hasselwander's* theory is hardly correct, for it is very unlikely that a rudimentary phalangeal element should be laid down as a peripheral tiny centre. A more likely explanation is that of a circumscribed inconstant differentiation in the common tarsale-metatarsale-phalanges primordium. The os interphalangeale should then belong to the group of accidental anomalies.

There may be reason here to compare the facts observed with those mentioned under os tibiale, where I likewise found a spur-shaped formation in certain cases. The latter was, however, accounted for on a phylogenetic basis.

That apparently alike formations may have different origins is not to be wondered at. Here — as elsewhere — the morphology is only the outer form of manifestation. And it appears

from my whole work that one and the same accessory bone may have different origins.

12. *Os subfibulare.*

The os subfibulare likewise seems to be a bone found only in man, and here even rarely. According to the literature it has never been observed histo-embryologically.

The bone is first described as such by *Leimbach* 1938, who has observed it radiographically, but does not account for its presence. Similar observations have previously been made, however, but have not been mentioned in relation to the question of accessory bones.

Thus *Schulte-Tenckhoff* 1929 has reported a radiographical finding corresponding exactly to the os subfibulare. The bone was observed in a man, aged 50, who 10 years previously had had both feet run over (nothing further). An X-ray examination now revealed fracture of the talus in the right foot, and in the left a cherry-sized detached bone under the tip of the fibular malleolus. The bone, which was removed by operation, proved to lie detached in the talocrural joint. This author explains his finding as a non-healed-up bursting fracture, where the fragment has grown secondarily.

Güntz 1942, who has demonstrated the os subfibulare radiographically, believes it to be a tendon bone developed in the peroneus tendon. To this may be added that *Lunghetti* 1909 has demonstrated the presence of a fibrous sesamoid nodule in the peroneus longus tendon on a level with the fibular malleolus, a fact which adds support to the hypothesis that the os subfibulare may in certain cases be regarded as a tendon bone. (As for tendon bones, see p. 202 *et seq.* under secondary bone formations).

Two more genetic possibilities will be discussed on the basis of own investigations.

As mentioned p. 82, I have once, unilaterally, found a hyaline-cartilaginous element at the site of the os subfibulare. On the basis of the development of the foot of the living mammal from the elements of the primitive tetrapod foot (p. 151, Fig. 122, and p. 152, Fig. 124) there is found no primitive element to account for its existence. My finding must, therefore, be regarded as an accidental anomaly.

I have often found a spur-shaped formation as an outgrowth from the tip of the fibular malleolus (*vide* Fig. 105, p. 94), but never detachment of the process. The possibility of such a detachment is, however, obvious, when we bear in mind the conditions observed with regard to the os interphalangeale.

13. *Os trigonum*.

Besides in man, a bone corresponding to the os trigonum has been observed also in marsupials (mammals) (*Bardeleben* 1883 and 1884, *Baur* 1885 and 1886, *Emery* 1894—1897, and *Lazarus* 1896), and also once in the horse (ungulata — mammals), indeed, only in synostosis with the talus (*Kassianenko* 1935). Apart from these cases I have found no mention of it in the literature.

Various histo-embryological investigations have been published, carried out both on human and animal feet.

Bardeleben 1883, 1884, and 1885 is the author and advocate of the theory of the os trigonum as a phylogenetic bone. In his paper from 1883 he claims to have seen the talus consist of 2 independent elements in human embryos, i. e. a distal element, explained as tibiale (in 1885 as centrale 1) and a proximal, explained as intermedium and regarded as the os trigonum preformed in hyaline cartilage. Of this intermedium he only states that it is triangular with its base turning distally, and that it is strikingly large in proportion to the tibiale (his later centrale 1) and the fibulare. Later the intermedium fuses with the remaining talus primordium. If now there occurs, within the ossification period, an independent ossification centre for the original proximal element, the result may be an os trigonum.

Furthermore *Bardeleben* succeeded, on an anatomical basis, in finding an element corresponding to the os trigonum in many marsupials (mammals). By comparing these findings with the fact that the intermedium is found as an independent element in urodeles (amphibians) *Bardeleben* claims to have proved that his explanation of the conditions in human embryos is correct.

However, by the end of 1885 *Bardeleben* himself invalidates his findings and explanation by suddenly, without further comments, setting up a new and different Table (*vide* p. 116), a fact of which no subsequent writers have made any remarks.

According to this latter Table the head of the talus is developed from the tarsale proximale 1 = tibiale, the body from the tarsale proximale 2 = intermedium 1, to which further the tarsale proximale 3 = intermedium 2 fuses in most cases, forming the processus posterior tali. He does not say which of these elements corresponds to his recently discovered finding from 1883. Neither does he give any information as to why he suddenly sets up an intermedium 1 and an intermedium 2.

In 1894 *Bardeleben* returns to his former view of the talus as developed from 2 elements, but now the proximal: fibulare and the distal: intermedium.

Baur 1885 and 1886 at first accepted *Bardeleben's* theory, but soon his own histo-embryological investigations, comprising all orders of mammals (including man) made him abandon this theory, because he failed to demonstrate more than one element for the talus.

Anatomically *Baur* has in many marsupials (mammals) found a bone corresponding to the os trigonum in adult humans, and in several marsupials, though not in all, he has found a similar independent hyaline-cartilaginous element at the pouch stage. *Baur* explains this element as a sesamoid bone.

Leboucq 1886 found no primordial os trigonum by examining a 12 mm. long human embryo, where the tarsal elements had been differentiated; but he adds, "il devient distinct, un peu plus tard, a l'extrémité proximale de l'astragale", and nothing more.

Emery 1894—1897 has examined both adult animals and embryos as well as pouch stages of marsupials and found conditions according exactly with those indicated by *Baur*.

Schomburg 1900 states that at the prochondral stage the talus proves to consist of 2 equally large elements, situated one behind the other. A little later he writes that the element described by *Bardeleben* has a few times been found by himself as comprising the most proximo-plantar portion of the talus. He has once found the processus posterior tali as an independent formation at the cartilage stage. Later he states, however, that the embryo was 9 weeks old, and simultaneously that the tarsal elements had a prochondral character.

Thus *Schomburg's* indications are not exact. He is also him-

self at a loss with regard to the explanation of the os trigonum, and he, therefore, desists from explaining it.

Haselwander 1914 has undertaken a serial-section analysis of embryos in the 1st and the 2nd month. He could demonstrate no independent hyaline-cartilaginous os trigonum, but he threw out a new problem by stating that the entire processus posterior tali presents a certain independence at the prochondral stage, without being quite detached, however. At a later stage this portion proves to be less vigorous than the remaining primordium of the talus, being finally completely absorbed by the latter. He states that the processus posterior tali has nothing to do with the intermedium, but he does not know exactly how to explain his findings.

Subsequent writers have not themselves studied the question of the genesis of the os trigonum, but found on the investigations published by others.

As mentioned p. 93, my own embryological investigations have never revealed an independent primordial os trigonum. Not even my small number of embryos from the prochondral stage displays any traces of such a primordium.

Bardeleben's theory of the human os trigonum as intermedium is refutable on the basis of the reports in the literature and own investigations. All the histo-embryological investigations of tetrapod feet — from the lowest to the highest — have shown that the perforating artery of the mesopodium runs between the intermedium and the fibulare through the so-called foramen interosseum = the tarsal canal (a. o. *Emery* 1894—1897, *Ihle*, *Kampen*, *Nierstrasz*, & *Versluys* 1927, *Schmidt-Ehrenberg* 1942, and *Ursing* 1932). That the same is the case in man has been shown a. o. by *Leboucq* 1886, *Schomburg* 1900, and through own investigations.

The intermedium must, therefore, either alone form the talus, or at least constitute an important component of it. It cannot be reduced to an indifferent rudimentary portion (*Emery* 1894—1897 and *Ursing* 1932).

According to the previously reported histo-embryological investigations (pp. 116—143) and *Steiner's*, *Schmidt-Ehrenberg's*, and *Holmgren's* explanation of the development of the foot of the living mammal from the elements of the primitive tetrapod foot (pp. 149—152) the talus must develop from 2 almost equally

large elements lying one behind the other, *viz.* the proximal: intermedium and the distal: centrale (possibly there are found 2 centralia situated side by side).

Bardeleben's findings also seem to establish the correctness of our present view of the talus as develop from 2 elements. As to his observations there is reason to remark that they were made on embryos in the 2nd month, i. e. at a stage where the differentiation in prochondral primordium of such a tiny bone as the os trigonum is hardly recognizable, at least not unquestionably so, and not with the addition that the element is strikingly large. As to *Bardeleben's* hypothesis from the end of 1885, I have found no facts to support it, so accordingly I cannot discuss it further.

Thus it appears from the above statements that the os trigonum cannot have developed from the intermedium, and accordingly not be of phylogenetic origin either, as the primitive tetrapod foot does not contain elements which might account for its existence.

It is, however, a given thing that the os trigonum is found in adult humans, and also that there is found a similar formation preformed in hyaline cartilage at the pouch stage of certain marsupials. How, then are these facts to be accounted for?

It is difficult to give an exact explanation. Most of the human cases should, I think, be explained as originally indicated by *Gruber*, that is as persistence of an inconstant ossification centre for the fibular tubercle of the processus posterior tali during the development of coalescence (*vide p. 195*).

The fact that *Hasselwander* 1903, 1910, and 1914 among 158 foot skeletons from the 3rd intra-uterine month till the 7th year of life did not in a single case find an independent hyaline-cartilaginous primordium of the os trigonum likewise argues in favour of this hypothesis. Between the ages of 8 and 11, on the other hand, *Hasselwander* has, in ab. one-third of his cases, seen development of an independent ossification centre for the fibular tubercle of the processus posterior tali. He, therefore, explains the os trigonum as a persisting epiphysis (*vide p. 195*).

Gruber's view is furthermore supported by the fact that the hyaline cartilage on the plantar surface of the talus in many cases is continuous with that on the os trigonum (demonstrated already by *Stieda* 1869).

This genesis does not explain, however, why the os trigonum is found as an independent primordium at the pouch stage in certain marsupials (and perhaps in man; cf. *Schomburg's* doubtful findings). If these findings were based on systematic serial-section analyses, which alone are conclusive (cf. own investigations p. 93) I think the hyaline-cartilaginous primordium concerned should be explained as a simple detachment of a particularly long fibular tuberosity of the processus posterior tali.

None of the theories of genesis propose explain why the percentage frequency of the os trigonum increases with increasing age, as shown by *Fischer* 1912—1913 to be the case. *Fischer* found the following figures on the basis of X-ray examinations of 500 cases:

Between the ages of 12 and 20 the os trigonum is found in 1.85%, between the ages of 12 and 25 the os trigonum is found in 4.84%, between the ages of 21 and 30 the os trigonum is found in 7.00%, between the ages of 31 and 40 the os trigonum is found in 6.6%, between the ages of 41 and 50 the os trigonum is found in 11.6%, between the ages of 51 and 60 the os trigonum is found in 17.34%.

The os trigonum may, therefore, also have a genesis differing from those suggested above. I think particularly of ossification in the ligamentum talo fibulare posterior, as also advocated by *Rabl* 1910 (*vide* p. 202) and fracture of the fibular tubercle of the processus posterior tali with pseudarthrosis formation, suggested a. o. by *Lilienfeld* 1906 (*vide* p. 213).

14. *Os Vesalianum*.

The os Vesalianum has to my knowledge been mentioned only in descriptions of human feet. (As to the conclusions to be drawn from this fact see p. 153, under os metatarsale I). Whether the bone can be said to be present in reptiles and amphibians depends on the genesis one attributes to the os Vesalianum, as will appear from the following.

Personally I have not found an independent primordium of the os Vesalianum on histo-embryological examinations, and, as far as I have been able to make out, only one such case in man has been described so far in the literature, by *Spronck* 1887.

It was a case of a new-born child, where the tuberosity of the 5th metatarsal is found as an independent element in the

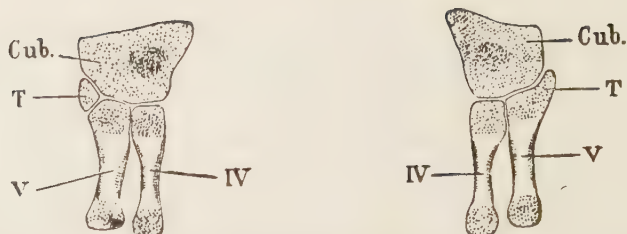


Fig. 126. (After Spronck 1887). Unilateral demonstration of an os Vesalianum as an independent hyaline-cartilaginous element in a new-born child.

right foot, while in the left it fuses, as usual, with the 5th metatarsal (unfortunately the child presented different deformities as well: on both feet 7 toes, but only 5 metatarsals, the 1st and 5th metatarsals each having 2 distal phalanges; furthermore, polydactylism of both hands, as well as harelip and cleft palate).

However, an independent element in the corresponding place has been found histo-embryologically in other mammals: mice (rodentia — mammals) (*Holmgren* 1933), *phascolarctus cinereus* and *aepyprymus rufescens* (marsupialia — mammals) (*Emery* 1894—1897), and *didelphys marsupialis* (marsupialia — mammals) (*Schmidt-Ehrenberg* 1942). All the writers state that the element has not been found as an independent bone in the adult animal. In these mammals the element is explained as being the tarsale distale 5.

Is the tarsale distale 5 found within other vertebrates?

Lutz 1942 found it histo-embryologically — but as a rudiment — both in *dromiceius novaehollandiae* (birds) and *anas boscas* var. *domestica* (birds). *Steiner* 1934 found it in *caiman crocodilus* (reptiles), *Holmgren* 1933 in *pelobates fuscus*, *xenopus laevis*, and *rana temporaria* (anura — amphibians), *Schmalhausen* 1910 in *salamandrella kayserlingii* (urodela — amphibians), *Steiner* 1920—1921 in *amblystoma tigrinum* (urodela — amphibians), and *Steiner* 1922 and 1934 in *cryptobranchus japonicus* (urodela — amphibians). Among various amphibians it is found as an independent element also in adults (*Broom* 1921, *Bütschli* 1921, *Gegenbaur* 1864, *Steiner* 1920—1921, and *Wiedersheim* 1876). It has likewise been found among reptiles, e. g. in *stereosternum* (*Rabl* 1910).

The question is now what becomes of the tarsale distale 5 in the cases where it is laid down in the embryo, but not found

in the adult animal. It has so far been a generally adopted view that it fuses with the tarsale distale 4 to form the cuboid, this bone articulating with both the 4th and the 5th metatarsal.

The only histo-embryological investigations which argue definitely in favour of this theory are those made by *Schmalhausen* 1910 on *salamandrella kayserlingii*. He found in larvae the tarsale distale 5 to be now independent and now more or less united with the tarsale distale 4. In adults it seems always to be completely united with the tarsale distale 4.

Holmgren 1933 states that in mice (rodentia — mammals) the tarsale distale 4 and the tarsale distale 5 always fuse already "as blastemas". This hypothesis does not seem to be based on own observations.

However, there are various facts which go against the theory that the cuboid should develop from the tarsale distale 4 plus the tarsale distale 5. For instance it has been shown in reptiles (*Sewertzoff* 1908 and *Rabl* 1910) and mammals (sus, *Suschkina-Popowa* 1915, *tarsius spectrum*, *Henckel* 1930, and *microcebus myoxinus*, *Schmidt-Ehrenberg* 1942) that primarily only the 4th metatarsal articulates with the element corresponding to the future cuboid, while the articulation of the 5th metatarsal with the cuboid element is secondary. Furthermore, these writers have not reported a single embryological finding showing only the slightest signs that the cuboid should have developed by fusion of the tarsale distale 4 with the tarsale distale 5. These findings correspond exactly to what I have observed in my embryos from the prochondral stage (*vide* Figs. 59 and 60, p. 61 and p. 62).

To this may further be added that investigations by *Sewertzoff* 1908 on reptiles, *Schmalhausen* 1908 and *Suschkina-Popowa* 1915 on sus (ungulata — mammals), *Suschkina-Popowa* 1915 on bos (ungulata — mammals), and *Holmgren* 1933 on vertebrates in the general show that the ray of tarsale — metatarsale — phalanges is formed by successive differentiation from a common prochondral primordium, independent of the tarsus.

In man the cuboid seems never to have been found as a bipartite formation. The only writer who mentions such an element is *Blandin* 1826 and 1834, but only in passing and in vague and incomprehensible sentences. Thus 1826: " — — ainsi nous avons rencontré deux fois sur la cadavre quatre os

cunéiformes, le cuboïde ne correspondait qu'au dernier métatarsien", and 1834: " — — le cuboïde, en quelque sorte divisé en deux os secondaires, ne correspondait qu'au dernier métatarsien". *Pfitzner* 1896 is definitely in opposition to *Blandin*.

Development of the cuboid exclusively from the tarsale distale 4 seems, therefore, the most likely explanation, the more so because the convincingness of *Schmalhausen's* findings are invalidated by the final result of *Holmgren's* investigations to the effect that "anurans, reptiles, birds and mammals belong to a tetrapod group which has originated from fish ancestors, probably crossopterygians with dichotomically branched pectoral fin skeleton, whereas the urodeles must be considered to have originated from fish ancestors, (crossopterygian or) dipnoan, with a short biserially arranged archipterygium".

The os Vesalianum can thus be explained as originating from the tarsale distale 5, as suggested already in 1921 by *Baastrup*.

We know of the tarsale distale 5 that it may either be differentiated from the above-mentioned prochondral primordium and persist as an independent element in the adult animal (amphibians) or be differentiated, but as a rudiment, to disappear again, possibly to fuse with the 5th metatarsal (cf. the mammals and reptiles, where the tarsale distale 5 has been found histo-embryologically, but not in adults). Finally it may remain undifferentiated concealed in the base of the 5th metatarsal.

As a rare exception it may, however, in the latter case be differentiated and persist, whereby we get an os Vesalianum. Or it may only just betray its presence in the base of the 5th metatarsal by the occurrence of a larger or smaller independent ossification centre of more or less vitality. If now a persistent epiphysis develops in these cases (*vide* p. 195), we again get an os Vesalianum.

In case the other hypothesis concerning the development of the cuboid (by fusion of tarsale distale 4 with tarsale distale 5) be correct, the os Vesalianum can be explained as develop from the postminimus - tarsale distale 6. As mentioned pp. 139—143, this element is observed histo-embryologically as an independent formation only in amphibians, and it is also among these that it is found in the adult animal (*Schmalhausen* 1917).

Thus, it seems possible to explain the os Vesalianum on a phylogenetic basis as a bone which can be traced back to the

tarsale distale 5, possibly the postminimus = tarsale distale 6. This does not mean, however, that it may not have a different origin.

D. INHERITANCE OF ACCESSORY BONES PREFORMED IN HYALINE CARTILAGE

A question of great interest is that of possible inheritance of accessory bones preformed in hyaline cartilage. This question has only just been touched on in the literature. I have found the question dealt with only by *Francillon* 1932, *Mestern* 1934, and *Faber* 1937.

Francillon mentions a mother and her daughter with ossa tibialia. *Mestern* reports on a female with bilateral os tibiale, who had a sister with os tibiale in one foot, while the other presented synostosis between os tibiale and navicular. Radiographs of their mother's feet suggested bilateral synostosis between os tibiale and navicular.

Faber claims to have found ossa tibialia in 3 generations (cf. pedigree):

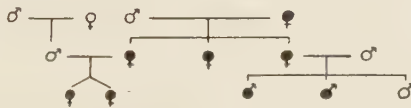


Fig. 127. *Faber's* 1937 radiographic findings of os tibiale in 3 generations.
● means bilateral finding, while ○ means no os tibiale.

Faber draws the conclusion that the os tibiale is due to a dominant gene.

The problem cannot be elucidated further on the basis of my material, because the parents of my embryos are unknown to me.

This question of possible inheritance of the accessory bones preformed in hyaline cartilage is, as already stated, a very interesting one. It is, however, somewhat difficult to answer it to satisfaction, since we cannot fully rely on radiography, partly because an accessory bone preformed in hyaline cartilage may disappear again, partly because it need not ossify, and partly because we may in the adult find a bone of a different genesis at the site of the hyaline-cartilaginous accessory bone (see the following sections).

II. DISCUSSION II: ACCESSORY BONES,
 INCONSTANT OSSIFICATION CENTRES,
 PERSISTING EPIPHYSES AND COALESCENCE

Even if an accessory bone is not demonstrable as an independent element at the cartilage stage it may nevertheless (according to *Parsons* 1903, 1904, 1905, and 1908, *Petri* 1935, and *Pfitzner* 1892 and 1895 and others) be of phylogenetic origin.

Pfitzner is of the opinion that inconstant ossification centres within one hyaline-cartilaginous primordium in many cases indicate the original independence of the part concerned. He admits, however, that such a demonstration is not conclusive. He has no proof of the correctness of his theory.

Parsons classes the epiphyses in three categories: pressure or articular epiphyses, traction epiphyses (on which tendons are inserted), and atavistic epiphyses. These latter epiphyses — which are of interest in this connection — are, in *Parsons'* opinion not preformed independently in hyaline cartilage; they do not betray their presence till the occurrence of a separate ossification centre, which should be due to the previous independence of this element.

Petri states, concerning fusion of the two primitive elements, that the following four things may happen:

1. a) The two elements are laid down independently; b) they fuse at the cartilage stage; c) there occur two ossification centres, revealing the originally division of the primordium; d) the two ossification centres fuse.

2. a) and b) like 1; c) there occurs only one ossification centre.

3. a) The two elements are not even laid down independently, but b) their presence is disclosed by the occurrence of two ossification centres; c) these two centres fuse.

4. a) like 3; b) only one ossification centre occurs.

Petri states, moreover, that not all the elements demonstrated to be formed early in the ontogeny need develop further. Some of them may either disappear again or persist as rudimentary formations.

Hasselwander 1903, on the other hand, claims occasionally to have ascertained two ossification centres within one zone of vesicular cartilage cells, so that in these cases there is actually only one ossification centre.

A. INCONSTANT CENTRES OF OSSIFICATION IN MAN AND MAMMALS

In order to give a survey of the inconstant ossification centres in the foot I shall briefly, for each bone, report a number of investigations dealing with the presence of these centres in *man*¹). (First the normal ossification centres are indicated in parentheses together with the periods of their presence, quoted after *Allen* 1926, *Béclard* 1819 and 1820, *Davies & Parsons* 1927, *Hasselwander* 1903, 1910, and 1938, *Rambaud & Renault* 1864, *Ruckensteiner* 1931, *Schwegel* 1858, and *Tandler* 1926).

The great variations in the points of time at which the individual ossification centres are stated to be present are (as remarked by *Hasselwander* 1938) due in a great measure to the fact that the early anatomical investigations for practical reasons comprised mainly children living in very bad social circumstances, and very often children who had long been seriously ill. In addition these investigators often lacked definite indications of age. Radiography has at a stroke changed the conditions of investigation, having also made it quite easy to examine thousands of normal children.

Furthermore it should be remarked that ossification centres occur earlier in females than in males (cf. *Åkerlund* 1918, *Davies & Parsons* 1927—1928, *Hasselwander* 1910 and 1921, *Kewenter* 1936, *Pryor* 1923 and 1927—1928, and *Sundt* 1942).

Sawtell 1931 states that inconstant ossification centres are of more frequent occurrence in boys than in girls.

A few animal investigations will be reported as a supplement to the above investigations. Here, too, the normal number of

¹) A knowledge of the inconstant ossification centres is also of practical clinical interest, as appears from the following case history (*Davis* 1927): A boy, aged 14, had his left foot run over by a motor-car. After radiography a diagnosis was made (elsewhere) of fracture of the base of the 5th metatarsal, and a compensation of 10,000 dollars was sued for. *Davis* now examined the patient, took radiographs of both feet and found corresponding conditions in the uninjured foot. He made a diagnosis of bilat. os Vesalianum, and the compensation fell away. (I must, however, object to *Davis*' explanation. The bone is not an os Vesalianum, but the at that age quite common shell-shaped fibulo-planto-basal epiphysis on the 5th metatarsal. vide p. 190).

ossification centres will be indicated first in parantheses. The following mammals have been investigated:

Guinea-pig (*cavia cobaya* — rodentia) by *Petri* 1935 (a number of embryos up to just before birth).

Mouse (*mus* — rodentia) by *Johnson* 1933 (8 embryos and ab. 35 new-born up to the 14th week), *Spark & Dawson* 1928 (388 animals pre- and postnatally).

Sloth (*bradypus tridactylus* — edentata) by *Ursing* 1932 (4 embryos and 2 young).

Dog (*canis familiaris* — carnivora) by *Schaeffer* 1934 (26 different stages from the earliest embryonic stage up to 18 months after birth).

Cat (*felis domestica* — carnivora) by *Schaeffer* 1932 (28 different stages from the earliest embryonic stage up to nearly 1 year after birth).

Ox (*bos taurus* — ruminantia — artiodactyla — ungulata) by *Küpfer & Schinz* 1923 (44 embryos and 3 new-born up to 13 days of age), *Petersen* 1922 (many embryos).

Hog (*sus* — non-ruminantia — artiodactyla — ungulata) by *Schinz* 1937 (1 new-born), *Surber* 1922 (a number of embryos up to birth).

Horse (*equus* — perissodactyla — ungulata) by *Saarni* 1921 (20 embryos up to birth), *Küpfer* 1931 (25 embryos and 3 new-born up to 7 weeks of age).

Donkey (*equus* — perissodactyla — ungulata) by *Küpfer* 1931 (29 embryos and 7 new-born up to 6 days).

Extremitas distalis tibiae.

(1 epiphyseal centre, generally present from the 6th postnatal month till the 2nd year of life).

An independent ossification centre for the tip of the malleolus has been found by *Béclard* 1819, *Cunningham* 1931, *Fairbank* 1922—1923, *Flecker* 1932, *Grashey* 1939, *Gray* 1918, *Hoed* 1925, *Lapidus* 1933, *Mouchet* 1923, *Rovida* 1927, *Ruckensteiner* 1931, and *Schwegel* 1858.

Mouchet has a fine illustration of this phenomenon. He took 3 radiographs of a boy, aged 12 years, at intervals of 6 months. The first showed a small centre, the second a larger centre, and the third complete fusion with the remaining epiphysis. *Hoed*, by X-ray examinations of ab. 150 children between the

ages of 6 and 12 years, found the centre in 21 cases, i. e. in 14 per cent.

Guinea-pig, mouse, sloth, dog, cat, ox, hog, horse, and donkey: (1 epiphyseal centre).

The cat may present an independent ossification centre for the tip of the malleolus (Schaeffer 1932).

Extremitas distalis tibiae.

(1 epiphyseal centre, generally present within the 1st to the 2nd year of life.

An independent ossification centre for the tip of the malleolus has been mentioned only by Schwegel 1858, who expressly states that all his ossification findings were made at least 3 times, generally 10 times or more.

Guinea-pig, mouse, sloth, dog, cat, ox, hog, horse, and donkey: (1 epiphyseal centre).

Calcaneum.

(1 primary ossification centre present from the 5th to the 7th intra-uterine month, and 1 posterior apophysis occurring from the 6th to the 12th year of life). Personally I did not find the primary ossification centre till the 27th week, i. e. the 7th intra-uterine month.

2 primary ossification centres were found by Sever 1930 in three cases in infants aged 2 years, 8 months, and 10 months respectively. Radiographs revealed 2 ossification centres situated one in prolongation of the other in the body of the calcaneum (bilaterally). The first infant was radiographed for control one year later, and there was now found only one centre. In the third case the calcaneum was submitted to histological examination. The bony tissue was found to be normal, the tissue connecting the 2 centres consisted of fibrous tissue, cartilage, and incipient bony tissue.

Perichondrial ossification centre. Hasselwander 1903 and 1938 has shown that a perichondrially situated centre develops on the fibular side of the calcaneum in ab. half of the embryos. This centre appears already within the 4th intra-uterine month, thus preceding the normal main centre. The two centres fuse

from the end of the 6th intra-uterine month. *Hintzsche* 1928 and 1930 has confirmed this finding histologically¹⁾.

My own histo-embryological investigations have likewise revealed this centre. As mentioned p. 103, I have calculated its frequency to be ab. 24 per cent. The centre is first observed in 14.6 mm. long feet, i. e. in embryos 14 to 15 weeks old, but here as a rare phenomenon. After the 16th week it reached the percentage frequency just indicated.

Hasselwander connects the centre with the trochlear process of the calcaneum, suggesting that it might be the cause of the calcaneus accessorius. *Hintzsche* disproves this hypothesis through his reconstruction models, showing that the perichondrial centre is not situated close to the trochlear process, but further proximally and in the plantar direction. I fully agree with *Hintzsche* (see also my histologic pictures p. 102 and p. 103, Figs. 117 and 118).

Several ossification centres in the posterior apophysis are of no rare occurrence. *Hasselwander* has observed up to 7 centres, fusing at an early stage, however. *Kirchner* 1907 has seen 2 centres, and *Ruckensteiner* 1931 up to 4.

Gelinsky 1904—1905, by X-ray examination of a boy, aged 15 years, found, in addition to the apophysis, a unilateral, apparently independent, lentil-sized ossification centre just proximal to the apophysis. This finding is possibly to be explained as an independent apophysis centre.

An independent ossification centre for the trochlear process is found anatomically by *Pfitzner* 1896 in a girl, aged 14 years, and by *Hasselwander* 1910 in 5 per cent. In 1932 *Francillon* demonstrated histologically that the finding in a girl, aged 11½ years, corresponds exactly to an epiphysis. Also *Friedl* 1924 has found such a centre by X-ray examination.

An independent ossification centre for the sustentaculum tali has been observed radiographically by *Güntz* 1934 in one foot of a girl, aged 10 years. *Hasselwander* 1910 has in one case found a partially fused epiphysis in this place.

¹⁾ In this place there is reason just to quote *Schomburg's* 1900 strange statement: In an embryo in the 8th week, of which he positively says that the tarsal elements have a prochondral character, he finds on the fibular side of the calcaneum "eine selbständige, aus verdichteten skeletogenen Zellen bestehende Knochenanlage", which he regards as having connection with *Pfitzner's* calcaneus accessorius. *Schomburg* dares not, however, pronounce with certainty on the question.

An independent ossification centre for the fibular process of the tuber calcanei has been found by *Hasselwander* 1910, *Kirchner* 1907, *Poland* 1898, and *Rambaud & Renault* 1864.

Guinea-pig, mouse, sloth, dog, cat, ox, hog, horse, and donkey: (1 primary ossification centre and 1 posterior apophysis).

The *mouse* may present an independent ossification centre for the trochlear process (*Spark & Dawson* 1928).

Talus.

(1 primary ossification centre, present from well over the 5th to the 8th intra-uterine month). Personally I did not observe the primary ossification centre till the 27th week, i. e. the 7th intra-uterine month.

2 or more primary ossification centres have been seen by *Hasselwander* 1903 and *Ruckensteiner* 1931. *Hasselwander* has found 2 centres, partly one above the other, and partly one in prolongation of the other. *Ruckensteiner* states that there are often found several centres, which, however, early fuse into 1 centre.

An independent ossification centre for the processus posterior tali has been found by *Gruber* 1864, *Hasselwander* 1910 and 1914, and *Laquerrière* 1933. Moreover, *Hasselwander* has repeatedly demonstrated the presence of a pseudo-epiphysis (*vide* p. 190 for explanation of this phenomenon).

Guinea-pig, mouse, sloth, dog, cat, ox, hog, horse, and donkey: (1 primary ossification centre).

Küpfer 1931 has occasionally in the *horse* found 2 primary centres situated one behind the other.

Os naviculare.

(1 primary ossification centre, present from birth till the 5th year of age).

2 or more primary ossification centres have been observed by *Cunningham* 1931, *Forsell* 1912, *Froelich* 1911, *Hasselwander* 1903, *Holland* 1928, *Rambaud & Renault* 1864, *Sawtell* 1931.

An independent ossification centre corresponding to the dorso-proximal edge has been found radiographically by *Françillon* 1934 and *Hasselwander* 1910.

An independent ossification centre for the entire tuberosity

or part of it has been observed by *Froelich* 1913, *Gruber* 1871, *Hasselwander* 1910, and *Pfitzner* 1900. *Froelich* has extirpated the centre and some of the adjacent part of the navicular in a boy, aged 12 years. He found, by microscopy of the extirpated tissue, that it constituted a central portion of bony tissue surrounded by hyaline cartilage. On the tibial side there was found tendinous tissue from the tibialis posterior tendon. Unfortunately nothing certain is stated as to the connection between the bony tissue in the navicular and the centre in the process.

Guinea-pig, mouse, sloth, dog, cat, hog, and horse: (1 primary ossification centre).

Mouse: in addition 1 ossification centre for the accessorium. Moreover, there may be found a centre for a small process on the accessorium (*Spark & Dawson* 1928).

Ox: 2 primary centres in the element: os centro-tarsale IV.

Donkey: 2 primary centres situated side by side.

It may further be added that an independent ossification centre for the navicular tuberosity has been found in *gorilla* (hylobates — primates — mammals) (*Monahan* 1920) and *rock coney* (procavia — proboscidea — mammals) (*Ursing* 1934).

Os cuboideum.

(1 primary ossification centre, present from shortly before birth till 4 months of age).

2 or more primary ossification centres have been found by *Hasselwander* 1903 and 1910, *Pryor* 1923, and *Ruckensteiner* 1931. *Pryor* states of the ossification "that it shows a very irregular shaped centre of ossification, sometimes scattered over an area of 2 or 3 mm. In some instances it would be impossible to say which was the beginning point".

An independent ossification centre for the tibio-distal-dorsal corner has been observed by *Ferguson* 1932, bilaterally in a boy, aged 10 years.

Guinea-pig, mouse, sloth, dog, cat, hog, horse, and donkey: (1 primary ossification centre).

The cat may present 2 primary centres lying one behind the other.

Ox: 2 primary ossification centres for the element: os centro-tarsale IV.

Os cuneiforme I.

(1 primary ossification centre, present from shortly after birth till the 4th year of age).

2 primary ossification centres situated one above the other have been seen by *Flecker* 1932, *Hasselwander* 1903, *Heidsieck* 1936, and *Sawtell* 1931.

Guinea-pig, mouse, sloth, dog, cat, ox, hog, horse, and donkey: (1 primary ossification centre).

Dog: there may be found 2 primary centres situated one behind the other (*Schaeffer* 1934).

Horse: 1 primary ossification centre for the element: os tarsale I + II, according to *Saarni* 1921.

Os cuneiforme II.

(1 primary ossification centre, occurring from the 1st till the 4th year of life).

2 primary ossification centres have been seen by *Sawtell* 1931.

Guinea-pig, mouse, sloth, dog, cat, hog, horse, and donkey: (1 primary ossification centre).

Ox: 2 primary ossification centres in the element: os tarsale II + III.

Horse: 1 primary ossification centre for the element: os tarsale I + II, according to *Saarni* 1921.

Os cuneiforme III.

(1 primary ossification centre, occurring from the 5th intra-uterine month till the 4th year of life).

2 primary ossification centres have been seen by *Sawtell* 1931.

Guinea-pig, mouse, sloth, dog, cat, hog, horse, and donkey: (1 primary ossification centre).

Ox: 2 primary ossification centres for the element: os tarsale II + III.

Ossa metatarsalia.

(1 primary ossification centre, present from the 8th till the 12th intra-uterine week. 1 epiphyseal centre for each metatarsal (proximal to the 1st, and distal to the others), developing from the 2nd to the 8th year of life). Personally I found the primary ossification from the 11th week.

2 or 3 epiphyseal centres in the normal epiphyses have been found a. o. by *Grashey* 1912 and 1939, *Hasselwander* 1903, *Holland* 1928, *Poland* 1898, *Rambaud & Renault* 1864, and *Sawtell* 1931.

Pseudo-epiphyses, i. e. rudimentary epiphyses instead of the normal have been observed by *Grashey* 1912, *Hasselwander* 1903, 1910, and 1938, and *Poland* 1898.

A pseudo-epiphysis is an "epiphysis" connected with the diaphysis by a narrow bridge.

Finally it may happen that *no epiphyses develop*. The ossification then occurs by successive, massive ingrowth from the diaphysis (*Hasselwander*).

Epiphyses corresponding to the opposite ends of the normal have been found by *Colwell* 1927—1928, *Cruveilhier* 1851, *Poland* 1898, *Sawtell* 1931, and *Schwegel* 1858 (the latter writer even states that they are normal findings).

Here, too, there may be found *pseudo-epiphyses* (*Hasselwander* and *Poland*).

The secondary ossification centre for the tuberosity of the 5th metatarsal will have to be commented on separately. There are found 3 inconstant types:

1. A shell-shaped centre situated on the fibulo-plantar side (cf. foot-note p. 183). Writers like *Iselin*, and *Rigler & Eneboe*, and *Schouwey* even hold, on the basis of their X-ray examinations, that this centre is constantly present. It generally develops between the 11th and the 14th year of age. *Holland* has in radiographs seen it divided in 3 minor centres.

2. A centre comprising the entire tuberosity, and

3. A centre comprising only the process of the tuberosity.

We do not know for certain whether the three centres are continuous with one another, but, according to *Hasselwander's* and *Pfitzner's* anatomical investigations, this seems to be the case.

These different epiphyses have been observed by *Davies* 1927, *Froelich* 1913, *Geist* 1914, *Gelinsky* 1904—1905, *Grashey* 1912 and 1939, *Gruber* 1885, *Hasselwander* 1910, *Holland* 1920—1921 and 1928, *Iselin* 1908, *Kirchner* 1906 and 1907, *Köhler* 1939, *Laquerrière* 1933, *Lilienfeld* 1906, *Pfitzner* 1896 and 1900, *Rigler & Eneboe* 1937, and *Schouwey* 1912.

Guinea-pig: (1 primary ossification centre and 1 distal epi-

physeal centre for the 2nd, 3rd, and 4th metatarsals. For the rudimentary 5th metatarsal there is found only 1 primary centre).

Mouse: (1 primary ossification centre and 1 distal epiphyseal centre for each of the 2nd, 3rd, and 4th metatarsals. For the 1st metatarsal there is found 1 primary centre, 1 proximal and possibly 1 distal epiphyseal centre. For the 5th metatarsal there is found 1 primary centre, 1 distal, and 1 proximal centre).

Sloth: (1 primary ossification centre and 1 distal epiphyseal centre for each of the 2nd, 3rd, and 4th metatarsals. The rudimentary 1st metatarsal contains 1 primary centre and 1 proximal epiphyseal centre, while the rudimentary 5th metatarsal contains only 1 primary centre).

Dog and cat: (1 primary ossification centre and 1 distal epiphyseal centre for each of the 2nd, 3rd, 4th, and 5th metatarsals. The rudimentary 1st metatarsal contains 1 primary centre and possibly 1 distal and 1 proximal epiphyseal centre).

Ox: (2 primary ossification centres and 2 distal epiphyseal centres for 3rd plus 4th metatarsals. For the 2nd metatarsal there is found 1 primary centre).

Hog: (1 primary ossification centre and 1 distal epiphyseal centre for each of the 3rd and 4th metatarsals. For the 2nd and 5th metatarsals there is found 1 primary centre, possibly 1 distal epiphyseal centre).

Horse: (1 primary ossification centre and 1 distal and 1 proximal epiphyseal centre for the 3rd metatarsal. The 2nd and 4th metatarsals each have 1 primary centre and 1 proximal epiphyseal centre, possibly also 1 distal epiphyseal centre).

Donkey: (1 primary ossification centre and 1 distal and 1 proximal epiphyseal centre for the 3rd metatarsal, while the 2nd and 4th metatarsals have only 1 primary centre and 1 proximal epiphyseal centre).

Proximal phalanges.

(1 primary ossification centre, present in the 3rd intra-uterine month. 1 proximal epiphyseal centre, developing from the 2nd year of life). Personally I found the primary ossification centre from the 14th week.

2 epiphyseal centres in the normal epiphyses have been found

by Grashey 1939, Hasselwander 1903, Holland 1928, Poland 1898, Rambaud & Renault 1864, and Sawtell 1931.

Epiphyses corresponding to the opposite ends of the normal have been found by Schwegel 1858.

Hasselwander 1903 has repeatedly found *pseudo-epiphyses*.

Guinea-pig, mouse, sloth, dog, cat, ox, and hog: (1 primary ossification centre and 1 proximal epiphyseal centre).

Horse and donkey: (1 primary ossification centre and 1 proximal and 1 distal epiphyseal centre).

The *dog* sometimes presents 2 centres in the proximal epiphysis (Schaeffer 1934). The same is the case in hog, (Surber 1922). In the *ox* there may be found 1 distal epiphyseal centre (Petersen 1922).

Medial phalanges.

(1 primary ossification centre, present from the 4th intra-uterine month. 1 proximal epiphyseal centre, present from the 2nd year of life). Personally I found the primary ossification centre from the 18th week.

2 epiphyseal centres in the normal epiphyses have been found by Poland 1898, and Rambaud & Renault 1864.

Epiphyses corresponding to the opposite ends of the normal have been found by Schwegel 1858.

Hasselwander 1903 repeatedly observed *pseudo-epiphyses*.

No epiphyses whatever is no rare phenomenon either (Hasselwander 1903).

Guinea-pig, mouse, sloth, dog, cat, ox, hog, and horse present conditions corresponding exactly to those mentioned for proximal phalanges. The donkey has only 1 epiphyseal centre, which is situated proximally. The same is occasionally the case with the *horse*.

Terminal phalanges,

(1 primary ossification centre, present from the 9th intra-uterine week, including the terminal phalanx of the big toe. 1 proximal epiphyseal centre, present from the 2nd year of life). Personally I have found the primary ossification centre from the 11th week.

2 epiphyseal centres in the normal epiphyses have been seen by Poland 1898 and Rambaud & Renault 1864.

No epiphyses whatever is no rare phenomenon (*Hasselwander* 1903).

Guinea-pig, mouse, dog, cat, ox, hog, horse, and donkey: (1 primary ossification centre).

Sloth: (1 primary ossification centre and 1 proximal epiphyseal centre).

In *ox* and *horse* there is occasionally found 1 proximal epiphyseal centre as well (*Petersen* 1922 and *Saarni* 1921).

Metatarsophalangeal sesamoid bones.

(1 primary ossification centre, present from the 7th year of life in females and from the 9th year in males, *Kewenter* 1936).

2 or more primary ossification centres are of frequent occurrence, especially where the tibial sesamoid bones are concerned (*Kewenter* 1936).

Guinea-pig, mouse, dog, cat, ox, horse, and donkey: (1 primary ossification centre).

B. ACCESSORY BONES CORRESPONDING IN SITE TO INCONSTANT OSSIFICATION CENTRES

How many of the constant and inconstant secondary ossification centres are due to original, independent hyaline-cartilaginous primordia is a question which it is difficult to answer, as is also the question whether these primordia are of phylogenetic, neogenetic, or anomalous origin.

It is hardly likely that constant and inconstant ossification centres should be explainable exclusively as developed from original, independent hyaline-cartilaginous primordia. It seems more natural to regard them only as secondary centres developed independently of previous hyaline-cartilaginous elements. *Parsons* 1903, 1904, 1905, and 1908 mentions also pressure (or articular) epiphyses, *Kirchner* 1906 and 1907 reckons with the existence of epiphyses of traumatic origin, and *Hasselwander* 1910, 1914, and 1921 with epiphyses caused by endocrine disturbances.

These, and possible other, hypotheses concerning the genesis of epiphyses are no more than conjectures; nothing certain is known as yet. Only it seems to be a fact that secondary ossification centres are not traceable to the primitive tetrapod foot,

but must have developed far later. Not even living reptiles and amphibians present regular epiphyseal centres (*Rabl* 1910), only very occasionally they may present sporadic, independent epiphyseal ossification (*Haines* 1938).

It is not known for certain whether ossification takes place at all in the primitive tetrapod foot. One thing is certain, however, that many elements, ossified in the feet of living animals, persist as cartilaginous elements in primitive and extinct animals. This fact renders it more difficult to pronounce on the construction of the feet of these latter animals, because cartilage is perishable to a greater extent than bone. According to *Böker's* "Schwielen"-theory 1927 ossification — both in epiphyses and in diaphyses — can be explained as an expedient adaptation to changed conditions of life.

By comparing the sites of the different accessory bones with those of the inconstant ossification centres it appears that the following accessory bones are situated in places which may correspond to inconstant ossification centres, and, therefore, perhaps explainable through these:

- calcaneus accessorius,
- os cuneiforme I bipartitum,
- os cuneo-metatarsale I plantare,
- os naviculare bipartitum,
- os sesamoideum partitum metatarso-phalangeale,
- os subfibulare,
- os subtibiale,
- os sustentaculi proprium,
- os talo-naviculare dorsale,
- os tibiale,
- os trigonum,
- os tuberis calcanei,
- os Vesalianum.

Of these accessory bones the following 4 may, according to their sites, correspond to elements in the primitive tetrapod foot: os naviculare bipartitum, os subtibiale, os tibiale, and os Vesalianum. This again means that if the existence of these 4 accessory bones is due to the presence of inconstant ossification centres the phylogenetic origin of these centres cannot be denied.

As to the remaining 9 accessory bones it can only be said that

if they owe their existence to the presence of inconstant ossification centres, then these centres may either be due to originally present independent hyaline-cartilaginous primordia (neogenetic or anomalous), or be secondary ossification centres developed from an unknown cause, independently of previously present primordia.

C. PERSISTING EPIPHYSES AND COALESCENCE

A condition that inconstant ossification centres may explain the presence of accessory bones is that these centres do not always fuse to the remaining primordial bone¹).

Here we come to the question of persisting epiphyses and coalescence. *Pfitzner* 1891, 1892, 1895, 1896, and 1900 categorically denies the existence of persisting epiphyses, although various writers before him adhere exclusively to this theory. *Pfitzner* deals instead with another problem, namely that of coalescence. He maintains that the epiphyseal development and the process of coalescence are two distinct phenomena, distinguishable already to the naked eye. Both begin to occur about the same age, but while the former always leads to synostosis before the age of 25, the synostosis often fails to occur, either entirely or partially, in the process of coalescence. However, *Pfitzner* gives no explanation to the fact why the process is one of epiphyseal development and finally fusion in some cases and one of coalescence in others. He presumes — on the basis of a small number of investigations made on lower vertebrates — that the more perfect process of epiphyseal development is younger phylogenetically than the simpler process of coalescence.

The process of epiphyseal development occurs only within one hyaline-cartilaginous primordium (no matter whether this primarily constitutes an entity, or becomes so secondarily after fusion). When the ossification sets in the process of epiphyseal development presents a terminal stage, since the ossification stops at a certain point of time forming a closing, thin

¹) The 13 accessory bones mentioned p. 194 may, of course, also be supposed to owe their existence to the fact that the original independent hyaline-cartilaginous primordia underlying the inconstant ossification centres were here, as an exception, laid down and persisted as independent elements. This possibility has, however, been discussed p. 143 et seq.

compact layer. Next the synostosis proceeds by "einen Verschmelzung der beiderseitigen besonderen Anschlussschicht" (*Pfitzner* 1896 and 1900).

The process of coalescence occurs either within one hyaline-cartilaginous primordium (where a fusion of cartilaginous elements has already taken place) or between two hyaline-cartilaginous primordia. The process does not present a final stage of development with the beginning of ossification; a closing compact layer never develops, no matter whether synostosis takes place or not. The synostosis occurs "als einfaches Zusammenfließen" (*Pfitzner* 1896 and 1900).

The epiphyseal plate consists, as is well-known, of hyaline cartilage. The plate of coalescence (called so analogically), on the other hand, presents a variegated picture, consisting centrally of connective tissue, mainly tight and tendon-like, but locally loose, while peripherally it changes successively into vesiculofibrous tissue, fibrocartilage, and possibly hyaline cartilage. In addition there are generally found larger or smaller fissures. The adjacent bone ends are not lined by a compact layer, on the contrary there is continuity between fibrous tissue, connective tissue bones and lamellar bones (*Pfitzner* 1895 and 1896, *Francillon* 1932, and *Güntz* 1934).

Radiographically, however, the line of coalescence as well as the epiphyseal line are regular and well-defined against the adjacent bone. This is due to the fact that there is a sharp line of division between the calcified and the non-calcified tissue.

Some writers (e. g. *Fischer* 1912—1913 and *Grumbach* 1921) regard coalescence as a pseudarthrosis formation, while others (e. g. *Hasselwander* 1914 and 1921) hold that the persisting epiphyses are due to traumatic damage and transformation of the epiphyseal cartilage, which render fusion of the two ossification centres an impossibility.

Against *Fischer's* and *Grumbach's* views concerning the cause of coalescence goes the fact that follow-up examinations of patients with epiphyseal detachment from the long bones — where the epiphyses are not quite abnormally dislocated — never reveal failing coalescence (*Bergensfeldt* 1933, *Eliason & Ferguson* 1934, *Henrici* 1935, *Ireland* 1933, *Poland* 1898, and *Reimann* 1942). If an epiphyseal detachment were the cause of coalescence, we should in a certain number of cases find absence of

coalescence in the cases of little or no dislocation of the detached epiphysis.

My attitude towards the question of epiphysis, persisting epiphysis, and coalescence is based on the following facts:

1. The frequent occurrence of accessory bones in places where there are found independent ossification centres (cf. p. 194).

2. Inconstant ossification centres are far more frequent than accessory bones in the corresponding places, as shown a. o. by *Hasselwander* 1903 and 1910. *Hoed* 1925 finds an inconstant ossification centre for the tip of the tibial malleolus in 21 out of 150 cases (i. e. 14 per cent), while the corresponding accessory bone, the os subtibiale, is found radiographically by *Holle* 1938 in 12 out of 1000 cases (1.2 per cent). The difference is statistically significant¹).

3. Parallel findings in the two feet of adults, only there is a constant and an accessory bone in one foot, while the other presents a constant bone with a process corresponding to the accessory bone (cf. f. inst. *Pfizzner's* findings 1896 with regard to the os trigonum, and own radiographs of the os Vesalianum, p. 52, Figs. 53 and 54).

4. My own histo-embryological investigations preclude with certainty the presence of an independent hyaline-cartilaginous primordium of the os trigonum and the os sesamoideum partitum of the 1st metatarsophalangeal joint. *Gruber* 1864, *Hasselwander* 1910 and 1914, *Laquerrière* 1933, and *Kewenter* 1936 have demonstrated the presence of inconstant ossification centres in this place, and *Pfizzner* 1892, 1895, 1896, and 1900 has shown that the os trigonum and the os sesamoideum partitum possess typical plates of coalescence.

It can, therefore, be concluded on the basis of these facts that the process of coalescence may take place within one primary hyaline-cartilaginous element, and that the process may lead to a permanent separation of the inconstant and the constant ossification centres, under development of a coalescence.

¹) Similarly with regard to the patella. Thus *Hellmer* 1935 states that there are found two or more ossification centres in ab. half of the cases, while *Sundt* 1942 — on the basis of numerous radiographical statistics — indicates that a patella partita is present only in ab. 2 per cent. [That the patella partita is suddenly mentioned is due to the fact that the radiographic conditions (macroscopic as well as microscopic) of this abnormality correspond exactly to those of the os sesamoideum partitum (cf. *Sundt*)].

The phenomenon which writers before *Pfitzner* called persisting epiphysis is thus no doubt to be regarded as coalescence.

It is more difficult to indicate the reason for the occurrence of coalescence. I dare not pronounce with certainty on this question, since I have found no satisfactory systematic investigations reported in the literature, and I do not myself possess a material fit to answer it.

If *Pfitzner* is right in presuming that the process of coalescence is the original, primitive process, it is only natural that it should occur at inconstant ossification centres, because these must *a priori* be supposed to be less vigorous.

Another possibility is that the process of epiphyseal development is the normal development of an inconstant ossification centre, while the process of coalescence is due to a disturbance in the epiphyseal. The reason for the occurrence of coalescence might then be sought in the consequence of an overcharging of the hyaline cartilage of the epiphyseal plate. The theory is based on our present knowledge of the cause of arthrosis deformans (*vide Burckhardt* 1932, *Wiberg* 1942, *Hirsch* 1943 and 1944, *Bergstrand* 1944, and *Palmer* 1944). The facts will here be explained in detail.

In the cases where normally there is found no ossification centre corresponding to the tip of an osseous process, the pull of the tendons and ligaments inserted in this process is transferred to the elastic cartilage in an expedient, physiological manner, so that the power of resistance of the cartilage is not exceeded.

If now an inconstant ossification centre occurs in such an osseous process, the mechanical conditions will become unphysiological at once, because the remaining cartilage, i. e. the epiphyseal plate developed, is exposed to a greater charging. In most cases the cartilage seems able to stand it, since inconstant ossification centres are far more frequent than inconstant bones in the corresponding areas.

In a certain number of cases, however, the cartilage cannot stand this unphysiological overcharging. The power of resistance is exceeded, which results in regressive changes in the cartilage.

The changes are initiated by reduction and disappearance of the chondroitin-sulphuric acid. This leads to oedematous infil-

tration of the cartilage, which then increases in volume and becomes of a loose and soft consistency. If the irritant continues to act the tolerance limit, now being low, is exceeded, and the cartilage begins to fall to pieces. Vesicular cavities develop in its interior, and the fibrils are laid bare, burst, become detached, and are shed off.

(The following observations made by other investigators will be added here to show that the changes suggested above in the cartilage between the two ossification centres are not entirely gratuitous: 1) *Müller* 1924 has made experiments in which he shows that an abnormal tension in the epiphyseal cartilage leads to abnormal thickness of the latter, due to inhibition of the enchondral ossification. In addition he shows that the unphysiological overcharging causes development of fissure in the cartilage. The fissure is filled up secondarily by pseudarthrosis-like tissue. 2) *Hellmer* 1935, by histological investigations of patellae with more than one primary ossification centre (boy, aged 4½ years) or with primary and secondary centres (boy, aged 9 years), finds the hyaline cartilage between the ossification centres to present regressive changes in several places. 3) *Hirsch* 1944 has shown that an excessive mechanical strain reduces the elasticity of the cartilage. This elasticity being responsible for the circulation, and thus for the nutrition, in the cartilage, the latter suffers damage, as can be shown chemically by reduction of the amount of chondroitin-sulphuric acid).

Since the hyaline cartilage cannot regenerate¹⁾, the changes are compensated for by ingrowth of connective tissue and fibrocartilage. When the enchondral ossification reaches this compensatory tissue it stops without forming a closing compact layer. A coalescence has now developed, which may be total or partial, dependent on the extent of destruction of the intermediate cartilage.

The individual cases in which the plate of coalescence is stated to consist of hyaline cartilage (*Pfitzner* 1896) can also be explained on this basis. The regressive changes in the

¹⁾ Hyaline cartilage is unable to regenerate. This power is lost, because hyaline cartilage is so to speak maximally differentiated tissue. When it is damaged the changes cannot be compensated for by development of new hyaline cartilage. The changes will have to persist or/and be replaced by a compensatory tissue consisting of connective tissue, fibrocartilage, and possibly bony tissue (*Müller* 1929, *Öwre* 1936 and *Palmer* 1944).

hyaline cartilage have in these cases led only to oedema of the cartilage, but this has been sufficient to stop the epiphyseal development.

As already mentioned, these explanations to coalescence are theoretical only.

Finally, as regards the question of persisting epiphyses, *Pfitzner* is perhaps not right in denying their existence, for, in the cases of the constant epiphyses they seem to be observable in man under decidedly pathological conditions, e. g. the hormonal dysfunctions: cretinism, acromegaly, anterior pituitary dwarfism and gigantism, myxoedema. Open epiphyseal lines have been found up to the ages of 40 to 50 (*Schinz, Baensch, & Friedl* 1939). No histological examinations are made, however, to show whether these cases present completely undamaged epiphyseal plates, or whether it is here actually a question of coalescence.

Moreover, failing fusion of the large constant epiphyses to the diaphyses is well-known also from animal investigations. This has been shown among others by *Dawson* 1929, 1934, and 1935 for different genera and races of mice and rats. In these animals the epiphyses may 1) fuse entirely or 2) in part, or 3) they may persist. To group 2 belong the olecranon, the calcanean apophysis, the head of the femur, the greater trochanter of the femur; and to group 3 the head of the humerus, the distal epiphyses of the radius, ulna, and femur, and the proximal epiphyses of tibia and fibula. The epiphyses which fuse are generally those which fuse early in the other mammals, while reversely the persisting epiphyses are those which fuse late in the other mammals. *Dawson* has also submitted such persisting epiphyseal plates to histological examination and found them to be separated from the bone marrow by a continuous osseous layer, both against the epiphysis and against the diaphysis. In many cases the cartilage cells present degenerative changes, and there are found numerous fine fibrils in the cartilage (thus perhaps actually coalescence).

III. DISCUSSION III: ACCESSORY BONES AND SECONDARY BONE FORMATIONS

The accessory bones which, on account of the size of my histo-embryological material, can be said for certain not in the general to develop from hyaline-cartilaginous primordia are the following:

calcaneus secundarius,
os peroneum,
os sesamoideum partitum,
os trigonum.

Of these 4 bones the os sesamoideum partitum and the os trigonum have already been described in detail p. 156 and p. 173; but no plausible explanations have been given as yet to the calcaneus secundarius and the os peroneum.

Such will be given below, first of the os peroneum, since several thorough investigations have been carried through regarding this accessory bone. In this connection the os tibiale will be accounted for from a different angle than that mentioned p. 159.

1. *Os peroneum.*

Besides in man the os peroneum is reported to have been observed in the following animals:

cebus (*Blainville* 1841).

cercopithecus (*Manners-Smith* 1908 and *Retterer & Lelièvre* 1911).

hylobates (*Kohlbrügge* 1890—1891 and *Manners-Smith* 1908).

macacus (*Manners-Smith* 1908 and *Retterer & Lelièvre* 1911).

mycetes (*Bardeleben* 1885).

papio maimon (*Weidenreich* 1923).

pavia (*Güntz* 1942).

pithecus talapoin (*Blainville* 1841).

semnopithecus (*Manners-Smith* 1908).

Besides in these primates (mammals) the os peroneum has been found also in:

viverra (carnivora — mammals) (*Blainville* 1842).

As to the conclusions that may be drawn from these sporadic animal findings, see p. 153 under os intermetatarsale I.

As already mentioned (p. 73) my histo-embryological investigations have shown that the os peroneum does not occur at the hyaline cartilage stage with the same frequency as in

adult humans (0.4 per cent against 8 per cent). This result accords well with the observations of other writers, who have not found the bone preformed in hyaline cartilage, neither in human nor in animal embryos.

Hasselwander 1903 and 1910, who examined 822 feet of humans ranging in age from shortly before birth to 25 years, did not either find the bone preformed in hyaline cartilage.

Hasselwander's statement 1938 that the os peroneum does not occur till the age of 25 is not quite correct. I have personally seen instances of its presence in radiographs. But while the os peroneum is of rare occurrence in children, it becomes steadily more frequent with increasing age, as appears plainly from *Fischer's* investigations 1912—1913. *Fischer* set up the following Table on the basis of 520 X-ray examinations:

Between the ages of 12 and 20 the os peroneum is found in 1.1%, between the ages of 12 and 25 the os peroneum is found in 3.2%, between the ages of 21 and 30 the os peroneum is found in 3.7%, between the ages of 31 and 40 the os peroneum is found in 8.7%, between the ages of 41 and 50 the os peroneum is found in 10.5%, between the ages of 51 and 60 the os peroneum is found in 18.3%.

According to the above statements there is no evidence to suggest that the os peroneum should be preformed in hyaline cartilage¹⁾, neither in animals nor in humans (my isolated finding cannot overthrow this theory). Since, as already mentioned, there is found no inconstant ossification centres either in the area of the future bone, the genesis of the os peroneum must differ from these 2 possibilities.

Various investigations into the os peroneum, carried out a. o. by *Gillette* 1872, *Tornier* 1894, *Lunghetti* 1909, *Retterer & Lelièvre* 1911, *Retterer* 1920, and *Weidenreich* 1923, all tend in a certain direction. Of these investigations those reported by *Lunghetti*, *Retterer* et al., and *Weidenreich* will be further discussed.

Lunghetti submitted to microscopy the peroneus longus tendon of 80 humans, of whom 11 had not yet attained the age of puberty. In 79 of these individuals he found either a fibrous

¹⁾ I cannot but mention in this place that if the os peroneum had been found preformed in hyaline cartilage within the different vertebrates, there would have been a possibility of explaining it on a phylogenetic basis. It would then have been traceable to the tarsale distale 6 (= postminimus) of the primitive tetrapod foot.

thickening, a fibrosesamoid, in a place corresponding to the site of the os peroneum or an os peroneum. The latter was found in 17 out of 69 adults (9 in both feet, 6 in the right foot, and 2 in the left). In other words, he found an os peroneum in 26 out of 138 feet, i. e. 16.8 per cent. All the individuals presenting an os peroneum were over 50 years of age, except 2, aged 23 and 47 years respectively. In addition he found in a number of cases fibrosesamoids in the tendon on a level with the fibular malleolus and the trochlear process of the calcaneum.

Microscopically the fibrosesamoid appears as modified tendinous tissue, successively passing into ordinary tendinous tissue. The fibrosesamoid consists of a dense network of fibrils, among which there are found oval or spherical cells, so-called vesicular cells.

The fibrosesamoid ossifies in a certain number of cases. The tissue in the centre is transformed into fibrocartilage, which undergoes calcification. The ossification is brought about by ingrowth of vessels, partly as a metaplastic process, but chiefly as a neoplastic process.

It is thus the rule that hyaline cartilage is absent in the development of the os peroneum. In rare cases there are found small nodules of hyaline cartilage in the fibrosesamoid transformed into fibrocartilage.

Retterer & Lelièvre state that when the same area of a tendon is exposed to continuous friction or pressure — in addition to the pull — there may, according to the size of the irritant, occur a change of the tendinous tissue under the formation of vesiculofibrous tissue, cartilaginous tissue, and bony tissue. These writers investigated among others the peroneus longus tendon in man, where it bends round the fibular edge of the foot in a very small curve. This place is marked on the cuboid by a facet lined with typical hyaline cartilage. In adults there is found a thickening in this area of the peroneus longus tendon (many investigators even find a bone, an os peroneum; but no such bone was observed by *Retterer & Lelièvre* among their 15 specimens). This thickening presents externally ordinary tendinous tissue, and internally (towards the bone) vesiculofibrous tissue, i. e. a compact tissue consisting of large vesicular cells and bundles of closely interwoven fibrils. A vesicular fibrosesamoid is formed. In addition, they examined

the tendon from an infant well over 2 years of age and found a beginning thickening with fibrils at right angles to the tendinous fibrils, but no vesicular cells.

Furthermore, *Retterer & Lelièvre* examined the corresponding area of the peroneus longus tendon in a few adult monkeys (*cercopithecus nicticans* and *macacus sinicus*). In the tendon of the *cercopithecus* they found in the middle an osseous nucleus, lined on the external side by tendinous tissue and on the internal side by cartilaginous tissue. The surface against the cuboid was seen to be covered by articular cartilage. In the *macacus* the thickening consisted externally of tendinous tissue, and internally of hyaline cartilage. (*Pfitzner 1886* likewise found the internal surface lined with hyaline cartilage).

Finally they examined the corresponding area of the peroneus longus tendon in a dog and found only normal tendinous tissue.

Retterer & Lelièvre explain their findings in the manner that it depends exclusively on the size of the irritant whether we get tendinous, vesiculofibrous, cartilaginous, or bony tissue.

Retterer 1920 states that the nodule of the peroneus longus tendon consists of connective tissue or fibrous tissue in children and in individuals with sedentary work, whereas in most other adults it consists of vesiculofibrous tissue, which in those who use their lower extremities much is transformed into cartilaginous and bony tissue.

Weidenreich has examined the os peroneum from a man, aged 20 to 25 years, and here found a central lamellar bone enclosed in connective tissue bone, which again was lined with chondroid tissue. Nowhere did he find hyaline cartilage. The os peroneum is thus a tendon ossification preformed in connective tissue, which *Weidenreich* believes to develop in consequence of pressure or traction.

Weidenreich examined also the os peroneum from a monkey (*papio maimon L.*). He found a central lamellar bone enclosed first in calcified hyaline cartilage and next in hyaline cartilage lined with fibrocartilage. This was a case of enchondral ossification.

In my embryological material I have in no case found changes of a fibrosamoid character in the tendon of the peroneus longus muscle.

According to the above investigations the os peroneum should be formed in a primary tissue (tendinous tissue), which secondarily, in response to the action of irritants from without, is transformed into more resistant tissue.

The secondary connective tissue (described to some extent p. 148) is on the whole of common occurrence in tendinous, aponeurotic, ligamentous, and capsular tissues, these tissues being particularly exposed to increased mechanical strain. It is a well-known fact that a successive change often takes place in these tissues, with gradual transition from the original tissue to chondroid (vesicular) tissue, to fibrocartilage, and possibly to hyaline cartilage, these new-formed tissues being particularly resistant. The tissue thus transformed may lie as scattered cells or cell islands, or as well-defined formations. This change into secondary tissue is known within the entire animal world (*Schaffer* 1930).

Occasionally the action of the irritants may even lead to the formation of bony tissue. The bony tissue developed first is connective tissue bone, which is later replaced by lamellar bone (*Francillon* 1932, *Tornier* 1891 and 1894, and *Weidenreich* 1923). In case hyaline cartilage has developed, enchondral ossification may also take place. The development of bony tissue being of particular interest in this connection, a detailed account will be given of it in this place.

Tornier's works 1891 and 1894 will form the basis of a survey of the osseous formations belonging here. He has with great zeal studied these facts in numerous different mammals, and he writes as follows, "Weitaus die meisten Bänder des primitiven Säugetierfusses erleiden, währen sich dieser Fuss in seine höher entwickelten, zahlreichen Descendenten umbildet, derartige Verknöcherungen, und sie vor Allem sind es, welche den Füßen und Fussknochen der einzelnen Familien, Gattungen und Arten ihr charakteristisches Gepräge verleihen".

Tornier states that a ligament may begin to ossify either from one bone or simultaneously from both, or by development in the ligament of an independent, secondary ossification centre. The former way of ossification results in the formation of an osseous process, which may finally lead to articulation or synostosis with the other bone. A similar result is attained if the ossification takes place simultaneously from both bones. Finally,

ossification from a secondary ossification centre may likewise result in synostosis or articulation, with one or the other bone, or both. Such ossifications occur, however, not only in ligaments, but also in tendons, e. g. the peroneus longus tendon. Such accessory bones as calcaneus secundarius, os cuboideum secundarium, os paracuneiforme, os peroneum, and os tibiale develop, in *Tornier's* opinion in this manner. He goes definitely against *Bardeleben's* phylogenetic explanations.

Thus, *Tornier* distinguishes between 2 kinds of ossification in tendons and ligaments: 1) ossification at the place of insertion in continuity with the bone, and 2) ossification free in the tissue independently of the bone.

ad 1: In the case of man the spur on the calcaneum is probably the best known formation. It is the ossified aponeurosis of insertion for the plantar aponeurosis and the flexor digitorum brevis muscle on the calcaneum tuber. The spur consists primarily of connective tissue bone, which is secondarily replaced by lamellar bone (*Francillon's* finding 1932 in a man, aged 26). *Adams* 1911 states that in addition to the calcaneum spur there is almost regularly found ossification at the place of insertion of the Achilles tendon, and furthermore there are generally found accessory bones, such as calcaneus secundarius, os intermetatarsale I, os tibiale, and os trigonum.

Francillon 1932 has found this successive change by connective tissue bone to lamellar bone also in the retinaculum of the inferior peroneal muscles of a woman, aged 32.

In connection with the question of accessory bones such ossified tissue formations at the places of insertion become of interest only if they can become detached. This may happen, partly by fracture and consequent development of a pseudarthrosis, and partly (possibly) on account of the tension to which they are continuously exposed (*vide* p. 214).

ad 2: Ossification may occur also independently of the bone in tendons and ligaments. Such ossifications seem to reach their relatively greatest extension in the tendons of the legs of many birds, the tendons being here ossified over long stretches. The ossification is not present in the young, but develops later through calcification of the tissue under formation of connective tissue bone, which secondarily is replaced by lamellar bone (*Weidenreich* 1923 and 1930).

Such an enormous development of secondary bone is, however, hardly known in man, where small, well-defined bones are the general rule. It is these secondary bones in tendons and ligaments which are of interest in a discussion on accessory bones. They have been known for centuries and have been collected under the designation of sesamoid bones. This is actually a misrepresentation of facts, for originally (according to *Pfitzner* 1892) *Galen* applied the term sesamoid bone for the ossicles that may be present at the joints of fingers and toes, on account of the resemblance of these bones to the seed of a plant unknown in our times. Thus, while the term sesamoid bones originally applied to small meta(carpo)tarso-phalangeal and interphalangeal bones preformed in hyaline cartilage, they have within the past few centuries got to comprise a heterogeneous group of bones, denoting now all the bones which can be explained neither as transmitted nor as self-developed phenomena. In other words, we speak of "bones" and "sesamoid bones". The unaccountable phenomena have got a name by being banished to this "Rumpelkammer". *Pfitzner* adds chaffingly "Es ist dies also ein gleiches Princip, wie wenn die Kinder nach *Heinrich Heine* die Erscheinungen der Aussenwelt eintheilen in Dinge, die man essen kann, und Dinge die man nicht essen kann".

On the basis of the above investigations it seems reasonable to regard the os peroneum as a tendon bone, i. e. a secondary bone developed postnatally in response to localized irritants acting from without.

Previously (p. 149, where the development of the extremities is mentioned) the question has been considered of regarding certain secondary tissue formations as forerunners of neogenetic bones. Applied on the os peroneum this may lead to the fact that — in case it is found expedient from an evolutionary point of view — the os peroneum may at some future time (probably in thousands of eyars) have a chance of becoming a neogenetic inconstant bone, or perhaps even a neogenetic constant bone.

Whether my isolated finding of an os peroneum preformed in hyaline cartilage should be explained in this manner, or be regarded only as an accidental anomaly is a question which will have to be left unanswered.

2. *Os tibiale.*

The os tibiale is mentioned p. 159, where its phylogenetic origin is evidenced. However, it appears plainly from *Francillon's* histological investigations on man (1932 and 1933) that not all ossa tibialia have a phylogenetic genesis.

Francillon finds by operations that the os tibiale is now completely imbedded in the tibialis posterior tendon, and now found more or less outside it. In some cases histological examination revealed the "os" tibiale as a sesamoid nodule at the early stages, i. e. a thickening in the tendon, constructed of compact fibrous tissue, vesiculofibrous tissue, and fibrocartilage. At later stages he found calcifications as well, but not yet development of bone. The tissue connecting this element with the navicular consisted of normal tendinous tissue. At a still later stage the os tibiale is found to consist of spongy, lamellar bony tissue, surrounded in succession by connective tissue bone, fibrocartilage, vesiculofibrous cartilage, and a closing compact fibrous connective tissue. The fibres of the tibialis posterior tendon are in some cases seen to radiate into the os tibiale, but not so in other cases. *Francillon* himself states that his findings are in line with those of *Lunghetti* with regard to the os peroneum (*vide* p. 202).

This means, in other words, that the os tibiale may arise also as a tendon bone, being then acquisite.

3. *Calcaneus secundarius.*

Only few investigations have been made into the calcaneus secundarius.

This accessory bone I have found mentioned in descriptions not only of the human foot, but also of the feet of gibbon (hylobates — primates — mammals) and horse (equus — ungulata — mammals).

Kohlbrügge 1890—1891 states that, during his anatomical investigations made on gibbons, he once found a calcaneus secundarius. He is, however, inclined to regard it as a pseudarthrosis.

Kassianenko 1935, during anatomical investigations made on ab. 100 horses, finds a calcaneus secundarius twice — in two different horses. The bone is in both cases in synostosis with the calcaneum, yet easily distinguishable from it by a marked

line of junction. *Kassianenko* has, however, previously (1926) reported cases of independent calcaneus secundarius in horses.

The embryological investigations reported in the literature do not seem to have revealed any hyaline-cartilaginous elements that might be explained as calcaneus secundarius, neither in man nor in animal. My own embryological investigations have not revealed such elements either.

The same is the case with *Hasselwander* 1903 and 1910, who examined 822 human feet, ranging in age from just before birth till 25 years, without finding the calcaneus secundarius preformed in hyaline cartilage.

No investigations have been made with a view to finding out whether secondary cartilaginous and bony tissue may be observed in the area corresponding to the site of the calcaneus secundarius. Nevertheless I am of the opinion that this genesis gives the most reasonable explanation to the existence of the calcaneus secundarius. However, a traumatic origin cannot be excluded either (*vide* p. 213).

It is comprehensible that *Kassianenko* regards the calcaneus secundarius as a phylogenetic bone, but evidence is lacking, as will be shown in the following. I, too, have entertained ideas tending in the same direction as those of *Kassianenko*. But while *Kassianenko* supposes the original primitive element to be a centrale 3 (= centrale fibulare distale), I thought it to be a centrale 4 (= centrale fubulare proximale), since it must be regarded as evidenced that the centrale 3 forms part of the future navicular, whereas the part played by the centrale 4 in the feet of the living animal is somewhat uncertain (thus *Steiner* and *Schmidt-Ehrenberg* believe it to contribute to the formation of the head of the talus, see Fig. 122, p. 151, while *Holmgren* regards it as part of the calcaneum, see Fig. 124, p. 152).

That the calcaneus secundarius has not been found as an independent element preformed in hyaline cartilage is no proof against this theory, since the bone might very well betray its phylogenetic genesis only by occurring as an inconstant ossification centre (*vide* p. 182). This being not the case either — neither in man nor animal — the theory of the calcaneus secundarius as a bone of phylogenetic origin will have to be abandoned for want of evidence.

IV. DISCUSSION IV: ACCESSORY BONES AND PATHOLOGICAL BONY STRUCTURES

Although it is outside the scope of my definition of accessory bones, I shall conclude the description of my investigations into the origins of the accessory bones with pointing out a number of different pathological possibilities of the presence of such bones.

I have resolved to do so, because even if a detached bone element may at a certain point of time be known to have a pathological cause, this cause cannot always be definitely recognized years after the lesion has subsided or become stationary. In such cases one is therefore, in doubt with regard to the genesis. Accordingly a review of the underlying pathological lesions seems of no small interest.

Bony tissue may develop in numerous pathological conditions. There is hardly a place where bony tissue has not been observed. Many theories have been advanced in explanation of such ossifications, e.g. that they should be due to detached embryonal cells, displaced or torn-off periosteous slips, or osteoblasts circulating free in the blood.

According to *Leriche & Policard* 1926 and *Leriche* 1939 — to whose papers reference may be made — the above theories are of no value. These writers maintain, on the basis of experimental and clinical investigations, that ossification can take place only if there is found young, unspecific, oedematous connective tissue of the embryonal type together with calcium salts.

Levander 1934, 1940, and 1941 gives a somewhat different explanation, which, perhaps, after all does not differ so much from that proposed by *Leriche & Policard*. *Levander*, after intramuscular injections of an alcoholic extract of bony tissue, demonstrated development of cartilaginous and bony structures in the areas of injection (results which have later been verified by *Annersten* 1940 and *Bertelsen* 1944). In other words, a cell-free extract stimulates the tissue locally to renewed differentiation. *Levander* now sets up the hypothesis that the bone-forming agent (which must be supposed to be of a lipid, or possibly a steroid nature) is found in the circulating blood and is excreted through the kidneys. Development of bony tissue can be expected wherever an ossifiable environment arises in

the form of young, unspecific connective tissue in connection with a vascular lesion (which allows the substance to emerge from the blood stream).

It cannot be said for certain whether *Levander's* hypothesis is correct. The results of his experimental investigations are easily explainable on the basis of *Leriche & Policard's* theory.

It is expedient to divide the pathological bony structures in 3 subgroups: i.e. those connected with A) the bony system, B) the joints, and C) the soft tissue.

A. LESIONS ASSOCIATED WITH THE BONY SYSTEM

1. *Fractures.*

a. Recent minor fractures:

The recent minor fractures are in many cases difficult to differentiate from accessory bones.

By a minor fracture I understand such a fracture as gives rise to the formation of a peripheral, up to hazel-nut-sized detached element. The fracture will thus in most cases involve only a small part of the bone, but exceptions do occur, e. g. transverse fracture of a sesamoid bone. These different kinds of fracture will not here be dealt with in detail, but reference may be made to a few compilations by *Eiken* 1916, 1917, and 1918, *Müller* 1927, and *Lauge Hansen* 1942. When multiple fractures are found, large and small mixed together, the minor fractures become of no clinical interest (and thus of no importance in point of differential diagnosis from accessory bones).

The recent minor fractures are in most cases distinguishable from the accessory bones, when one is aware of the existence of these small bones.

The difficulty with regard to differential diagnosis generally arises when, by radiography of an injured foot, one finds an independent bony structure in more or less intimate relationship to one of the constant bones of the foot.

The past history and the clinical findings are of limited value as means to attain to a correct diagnosis. Thus, for instance, a false step may effect a "sprain" in the fibres connecting a unilateral accessory bone with the adjacent constant bone, resulting in swelling, extravasation of blood, tenderness,

and limited mobility (cf. *Güntz'* traumatic tearing off of the os tibiale, 1934). In such cases there are found both trauma, local symptoms, and unilateralism, but still there is no minor fracture.

The most important aids to the differentiation are the quality of the picture, bilateral examination, and repeated radiography. It is essential that the pictures are first-class. In doubtful cases radiographs should always be taken of both feet, and always from the most suitable aspects. Bilateral finding goes against a diagnosis of minor fracture. Unilateral findings indicate nothing (cf. my histo-embryological investigations as well as the genesis on the whole).

If a radiograph reveals a detached osseous element with a corresponding loss of substance in the adjacent bone, and if the meeting bone surfaces appear in profile to be sharp and without cortex, irregular and jagged, the picture is most likely one of minor fracture. Reversely a picture of a detached bone element with no corresponding loss of substance in the adjacent bone and with the meeting bone surfaces appearing in profile to be regular (rectilinear or curved) and well-defined this argues in favour of accessory bone.

It is by no means difficult to distinguish between a typical minor fracture and a typical accessory bone. But, as is important to know, a great number of cases are not typical. Both the fractures (in particular the tear-off fractures) and the accessory bones are often so small that they are only just recognizable as formations the size of the head of a good-sized pin. It is impossible to say whether these formations are due to fracture or not. In other cases it is impossible to picture the bounding surfaces sufficiently clearly, or to recognize a definite loss of substance in the adjacent bone.

In such doubtful cases one or more control examinations will generally be of aid, where a demonstrable callus formation or a change in the picture gives evidence of fracture.

A diagnosis of accessory bone is, of course, often difficult to make, if one does not have a thorough knowledge of accessory bones. But even with a knowledge of these bones a differential diagnosis between minor fracture and accessory bone is sometimes impossible to make.

An illustrative case is reported by *Paal* 1934: A man, aged 34,

had 5 radiographs taken of an injured foot by 5 different radiologists within $3\frac{1}{2}$ years, and the following diagnoses were made: 1) compression fracture of the navicular with disruption of a bean-sized dorsal wedge, 2) no fracture, but there is found an os tibiale, 3) as 1, 4) as 1, and 5) no fracture, but there is found an os talonaviculare dorsale. This latter diagnosis settled the question of insurance. (The data available make me adhere more to the first diagnosis).

b. Recent fractures of osseous spurs and osteophytes.

As to the question of recent fractures of spurs and osteophyte reference may be made to the facts already stated for minor fractures.

c. Long-standing, non-healed, minor fractures.

While the recent minor fractures most often are recognizable as such, things are different with the long-standing pseudarthrotic minor fractures, the latter being in many cases radiographically unrecognizable as such, because the meeting bone surfaces have become smoothed. Often it is also through anatomical and histological examinations impossible to say for certain whether one has to do with a long-standing fracture.

Mitterstiller 1923 and 1931 finds that the tissue between the bone ends consists of fibrous connective tissue, fibrocartilage, and hyaline cartilage, often with no sharp lines of division between the different tissues. In this tissue he finds, moreover, some oblong cavities visible to the naked eye. The meeting bone surfaces are smoothed, and the medullary cavity may be closed by spongy and compact bony tissue.

Similar findings have been reported by *Bier* 1923. In addition he states that pseudarthroses may be enclosed in a capsule, and that the joint thus formed may contain a fluid resembling synovia. Pseudarthroses may form perfectly regular diarthroses with capsule, ligaments, synovial membrane, synovia, and cartilaginous articular surfaces.

The fact that the tissue between the bone ends may consist of fibrous connective tissue, of cartilage, and — at the normal healing — of bony tissue is by no means extraordinary (according to *Leriche & Policard* 1926 and *Leriche* 1939), for the young, unspecific oedematous connective tissue of the embryo-

nal type, immediately developing at the site of fracture, can, under the right influence, form any kind of tissue within the connective tissue group.

In the daily routine it is not uncommon to meet with such accessory bones developed from long-standing, non-healed fractures. However, one cannot always be certain that the underlying fracture is remembered. This depends probably in the first instance on the troubles the fracture gave rise to when it occurred. An instance will be given here:

A woman, aged 43, jumped down on her right foot, twisted her ankle (outwards), and fell. Admitted to hospital 2 days later for other conditions. A radiograph was taken because of the past history, the swelling, and the tenderness round the tuberosity of the 5th metatarsal. The radiograph revealed a typical minor fracture with a burst-off tuberosity (the normal left foot presented no such bursting fracture). Was treated by a walking-plaster of paris for 4 weeks. The patient was re-examined 5 years later. The foot caused her no troubles. A control radiograph showed no osseous healing of the burst-off tuberosity, but the adjacent bone surfaces had now become smoothed and rounded, so that a diagnosis of fracture could not be made on the basis of this picture.

The development is evident in this case. If, however, the patient had not been examined and treated immediately after the trauma she would hardly have fixed her attention on the accident. A radiograph taken ab. 10 years later would then reveal a unilateral, independent bone, which would be diagnosed as an *os Vesalianum* of unknown origin, because in 9 out of 10 cases the patient would be unable to explain its existence.

According to various writers it is not only fractures which may give rise to pseudarthrosis-like findings. Müller 1924, in experiments on dogs, rabbits, and rats, has shown that abnormal continuous strain on a bone may gradually, in the course of some months, lead to an almost linear cleavage of the bone, histologically resembling pseudarthrosis.

Finally there is reason to mention that tearing off of periosteum, tendon, ligament, or capsule often gives rise to new bone formations, because the piece of bone torn off with the rest necroses and is resorbed under liberation of calcium salts. The conditions that new bones may develop are procured through

simultaneous organisation of the haematoma in the injured tissue by ingrowth of young, unspecific oedematous connective tissue of the embryonal type (*Leriche & Policard*). On the basis of *Levander's* 1934, 1940, and 1941 experiments the development of new bone may be explained as follows: the torn-off bony tissue dies, and unspecific mesenchymal tissue is formed. By the necrosis of the bony tissue a substance is liberated which is able to activate the unspecific mesenchymal tissue, so that cartilaginous and bony tissue may develop from it (*Leriche & Policard* 1929, and *Levander* 1940 have shown experimentally that periosteum as such is unable to form bony tissue).

The bone thus developed may either be resorbed or be altered and become stationary after having reached a certain size.

In the case of the knee-joint the pure tearing off of the capsule is known as *Stieda's* (or *Köhler-Pellegrini's*) disease. A thin detached shell of bone develops at the site of tearing 3 or 4 weeks after the trauma. Generally the detached bony tissue disappears again, however, within ab. one year.

Michelson 1930 reports a case regarded as one of *Stieda's* disease, but localized to the external side of the fibular malleolus (Fig. 25, p. 36).

2. Infections.

Inflammations may in certain cases give rise to division of bones or isolation of pieces of bone.

Bennet 1935 reports a case of *os sesamoideum partitum*, where the division proved to be due to unspecific osteomyelitis.

A circumscribed osteomyelitis may in certain cases lead to isolation of a small, well-defined osseous element presenting itself as an independent ossicle. *Smith* 1873 and *Kjærgaard* 1925—1926 describe unspecific cases of this kind, having found a pea-sized bone in a depression on the dorsal side of the neck of the talus. *Kienböck* 1938 reports a similar case, but of tuberculous origin. I have also personally seen such an — unspecific — case with isolation of a pea-sized osseous element from the dorsal side of the neck of the talus in a woman, aged 22.

3. Aseptic Necroses.

Various writers regard aseptic necrosis (or related lesions) as the cause of bone division.

This is the case with the os sesamoideum partitum, according to investigations by for instance *Renander* 1924, *Müller* 1925 and 1927, *Sundt* 1944, and with the os naviculare bipartitum, according to *Müller* 1927 and 1928, *Weiss* 1929, *Simons* 1930, *Wilke* 1930 and *Frosch* 1931 (*vide* besides p. 156 and 166 respectively):

4. Circumscribed Condensations.

It may be difficult in radiographs to differentiate circumscribed condensations from accessory bones. They resemble each other, only the former are not projected free of the adjacent constant bone. Of lesions giving rise to such condensations the following may be mentioned:

a) compact islands (Fig. 47, p. 49) (*Esau* 1934, *Fischer* 1912—1913, and *Stieda* 1905).

b) osteosclerosis disseminata familiaris = osteopoikili = osteosclerosis fragilis generalisata = ostitis condensa generalisata (*Busch* 1936)].

B. LESIONS AFFECTING THE ARTICULAR APPARATUS

Before an account is given of the different lesions in the articular apparatus it seems appropriate to report some details concerning the synovial membrane. This membrane forms the interior articular capsule.

There has long been disagreement as to the question whether the synovial membrane is separated from the articular cavity by epithelium (endothelium) or not. *Lubosch* 1910 maintains that such epithelium (endothelium) is never found in amphibians, reptiles, and birds, and that it has no phylogenetic origin. Modern investigators seem to agree that no epithelium (endothelium) exists in this place, and that the inner surface of the membrane is not smooth, but slightly rough (according to *Policard* 1936).

The synovial membrane is constructed of connective tissue cells varying considerably in appearance. (See for instance *Lubosch*' survey). Especially it should be mentioned that there are found cells and cell islands presenting all transitional stages to real cartilage cells (*Tourneux & Hermann* 1880, *Hammar* 1894, *Kroh* 1908, and *Lubosch* 1938). *Weichselbaum* 1877 even claims to have observed that in the part of the synovial mem-

brane bordering on the articular cartilage there is found continuous transition from synovial membrane by connective tissue cells to hyaline cartilage cells.

Weichselbaum states further that the senile changes in the synovial membrane manifest themselves among others by formation of cartilage cells and cartilage bodies developing from the normal cells.

Moreover, it has repeatedly been stated in the literature (e. g. by *Hagen-Torn* 1882 and *Burckhardt* 1932) that pressure may lead to formation of cartilage (*vide os peroneum* p. 202 et seq.).

Leriche & Brenckmann 1928 have shown through experiments that both extra- and intra-articular bony tissue may cause development of intrasynovial cartilage and bony tissue. It should also be mentioned that bone formation takes place in the synovial membrane under pathological conditions.

Lubosch' 1910 phylogenetic joint investigations made on vertebrates revealed facts which argue greatly in favour of the hypothesis that the synovial membrane is able to form cartilage cells and bodies. He arrives at the result that the synovial membrane originates phylogenetically from cartilage or fibrocartilage, being, therefore, historically predisposed to cartilage formation. The cartilaginous elements demonstrated in man must be explained as genuine atavistic formations.

The cells chipped off from the synovial membrane (and articular cartilage) during wear and tear may possibly live further, grow, calcify, and ossify. It is a well-known fact that the articular cartilage is nourished for the greater part by synovia (according to *Policard* 1936). Synovia may, accordingly, be conceived to nourish the chipped-off cells (*Bergstrand* 1944). Generally, however, they are fixed to the synovial membrane and decay (*Hultén & Gellerstedt* 1941)..

1. *Fractures.*

With regard to fractures the same phenomena assert themselves as mentioned pp. 211—215. It only remains to be added that joint fractures are particularly exposed to pseudarthrosis formation, because synovia has an inhibitory effect on the process of healing (*Bier* 1923).

2. Arthroses.

The most important arthrosis lesion is that of arthrosis deformans, which will, therefore, be taken as prototype. The following may be summed up regarding this lesion, on the basis of investigations by *Burckhardt* 1932, *Schinz*, *Baensch & Friedl* 1939, *Wiberg* 1942 and 1944, *Hirsch* 1943 and 1944, *Bergstrand* 1944, and *Palmer* 1944:

Arthrosis deformans is primarily localized in the articular cartilage. The changes are partly degenerative and partly proliferative.

The degenerative changes are localized in the first instance to the central areas of the articular cartilage, gradually causing more or less destruction of the latter. The changes in the cartilage begin with reduction and disappearance of the chondroitin-sulphuric acid. This leads to oedema, with a consequent increase in the volume of the cartilage, which becomes loose and soft. If the releasing factor continues to act the limit of tolerance of the cartilage — which is now low — is exceeded, and the cartilage begins to fall apart. Vesicular cavities develop inside the cartilage, and the fibrils are laid bare, burst, detach themselves, and are shed off. Defects occur which may extend so deep that the underlying bony tissue may be laid open.

The proliferative changes occur particularly along the marginal zone of the cartilage, giving rise to development of so-called marginal outgrowths (not osteophytes, as they were previously called, such being of periosteal origin, *Burckhardt* 1932).

The shock- and pressure-absorbing effect of the cartilage on the bone is lost because of the cartilage degeneration. Consequently reactive changes occur in the bone, of a resorptive as well as a constructive nature (excrescences, cavities, and eburnation).

Finally the synovial capsule is also involved (the changes found here are not primary, but are present only in association with well-pronounced cartilage-bone changes). The synovial membrane becomes hyperaemic, the cells proliferate, and papillary excrescences are formed, penetrating into the articular cavity. These excrescences consist of connective, fatty, cartilaginous, and bony tissue. The fibrous capsule becomes

thickened, and in this there may likewise occur calcification and ossification.

Detached joint mice may also be formed, derived partly from torn-off cartilage, partly from the bone surface which is laid bare, partly from the marginal outgrowths, and partly from the capsular excrescences. Microscopically they are found to consist of a mixture of connective tissue, fibrocartilage, hyaline cartilage, calcified tissue, and bony tissue (*Hahn* 1919).

It should be pointed out that when detached joint mice and capsular bones are found in association with arthrosis deformans, there are always found more than one in the same joint, generally many, and the joint concerned will at the same time present pronounced bone changes (*Burckhardt* 1932).

The other forms of arthrosis present similar pictures, only the changes are more pronounced in the cases of neuropathic articular lesions, being here almost caricatures of those mentioned above.

The aetiology of arthrosis is not quite clear. The lesion seems in many cases to develop on account of a static-mechanical disproportion (possibly on the basis of a constitutional factor). The power of resistance of the cartilage should thereby be exceeded, and this again should lead to the degenerative changes. The fact that a mechanical disproportion may lead to such changes is by *Hirsch* 1944 explained in the following manner: Overcharging of the cartilage reduces its elasticity. The elasticity being responsible for the circulation, and consequently for the nutrition, the cartilage suffers damage. This may manifest itself chemically by a reduction of the amount of chondroitin-sulphuric acid. The power of resistance may be exceeded in connection with hyperfunction — even at a normal function, if the resistance is subnormal, for instance because of disturbances of nutrition — but above all in connection with a function which is not quite physiological, but has the character of a dysfunction. It is important to know that arthrosis may be seen also in young individuals, and even in children (*Pitzen* 1927).

Arthrosis is often seen to develop in association with subluxation of the hipjoint, flatfoot, intra-articular fractures, recurrent articular haemorrhage, aseptic bone necrosis, and arthritis. Also endocrine disturbances (especially in connection with the

menopause and metabolic diseases) and nervous diseases may be attended by arthrosis. Finally there are found cases in which no cause can be demonstrated. The occurrence is here supposed to be due to ordinary wear and tear, and to tissue degeneration.

Pitzen 1927 and *Hohman* 1934 report many cases of arthrosis deformans in the joints of the foot. Often only one or a few joints are affected. The light cases present only slight tapering of the articular borders. In the talonavicular joint and in the joint of tibial cuneiform and 1st metatarsal we may find osseous processes corresponding exactly to that which many writers call fused accessory bones.

Whether *chondromalacia patellae* = traumatische Knorpelrisse = fissurale Knorpeldegeneration = chondropathia traumatica = chondromalacia posttraumatica is a forerunner of arthrosis deformans is a question which cannot be definitely answered. *Öwre* 1936, *Wiberg* 1942, and *Hirsch* 1943 and 1944 think it likely to be so, because the disease presents a pathologico-anatomical picture resembling that of arthrosis.

Chondromalacia is a cartilaginous disease occurring in the patella. In rare cases the patellar surface of the femur is involved or affected alone (*Aleman* 1928, *Müller* 1929, *Friberg* 1940, *Karlsson* 1940). It is the general rule that the basal cartilaginous layers are not involved (*Aleman* 1928, *Müller* 1929, *Silfverskiöld* 1938 and *Lang* 1943), but exceptions do occur (*Öwre* 1936).

The disease generally affects young individuals about the age of 20; but also children down to the age of 11 have been seen to suffer from the disease (*Silfverskiöld* 1938). Most writers regard the disease as developed on a traumatic basis. The trauma, which may be either a single greater trauma or repeated minor ones, often of several years' duration, brings about a rupture of the cartilage, which is the lesion underlying the subsequent disease (cf. *Aleman* 1928 and *Karlsson* 1940). A few investigators (e. g. *Öwre* 1936) deny the influence of traumas.

It is expedient to divide chondromalacia in a latent and a manifest form, for it appears that postmortem examinations in many cases reveal cartilaginous changes, even though there

have been neither symptoms nor clinical signs of such. *Aleman* 1928, for instance, found latent chondromalacia in one-third of his 220 cases submitted to arthrotomy (done for other conditions on soldiers about the age of 20). *Öwre* 1936, by post-mortem examination of apparently normal knees, found latent chondromalacia within all age-classes, but increasing in frequency with increasing age, being constant after the age of 40 to 50.

3. *Arthromas.*

The articular tumours may be divided in benign and malignant tumours. The latter are extremely rare and of no interest here. Articular chondromatosis is the best known form of benign tumours.

a. Articular chondromatosis:

According to current descriptions (*Burckhardt* 1932, *Kienböck* 1938, *Schinz, Baensch, & Friedl* 1939, and *Radner* 1941) articular chondromatosis is a rare disease affecting chiefly adult men. It is most often monarticular, rarely diarticular (then generally involving symmetrical joints), and never polyarticular. The following joints of the foot have been found affected: ankle joint, proximal joint of big toe, and once the joint between the 3rd and 4th metatarsals (*Bentzon* 1930).

The articular chondromatosis may be situated in any part of the joint, i. e. the fibrous capsule, the synovial membrane, and the articular bone. A distinction is made between fixed bone chondromas and movable capsule chondromas. The latter may be intra-, inter-, or extracapsular, and finally they may be found as joint mice. The osseous form, the capsular form or both forms may be present simultaneously in one patient.

The aetiology is unknown. The disease is generally regarded as a benign multiple tumour formation. Most investigators believe that numerous hyaline cartilage nodules develop, from causes still unknown, in the synovial membrane, and particularly its villi. These nodules grow till they are pea- or nut-sized. Subsequently they will calcify. Some of them undergo ossification, forming small osteochondromas. The nodules become pendulous gradually as they grow in size; the stalk becomes longer and longer, and the nodules are finally in most cases knocked off into the joint.

Nothing certain is known as to whether the cartilaginous nodules arise in the somewhat problematic cartilage cells normally present in the synovial membrane.

Also other views have been advanced concerning the aetiology. *Beckman & Iverson* 1928 state that the hyaline cartilage islands develop in the deep layers of the synovial membrane, while the superficial layers present signs of inflammation. Thus there is no reason to regard the disease as a tumour.

Yet another view has been advanced by *Brenckmann* 1927, who states that the great majority of the nodules are detached bodies, no matter whether they are small or big, and that the synovial membrane is normal as a rule. *Brenckmann* is, therefore, of the opinion that the nodules do not develop in the synovial membrane. He believes them to be formed along the borderline between synovial membrane and synovia, when, from unknown causes, there occurs a disturbance of equilibrium in the colloids of the synovia and the collagenic substance in the inmost synovial membrane layer, which is imbibed with synovia. This will result in a precipitation of hyaline cartilage substance round the myxoidally transformed synovial membrane cells. The new-formed cartilaginous nodules are easily detached from the loose and not very resistant myxoid tissue during the movements of the joint. They rarely become fixed where they are formed. Secondly, on the other hand, the detached bodies may become fixed to the synovial membrane, that is when they lie immobilized in articular recesses.

According to *Brenckmann* the detached bodies consist at the first stage of hyaline cartilage. Gradually these bodies become enclosed in several layers of fibrocartilage, which in part undergo calcification. The fibrocartilage layers are again at a still later stage surrounded to a greater or smaller extent by connective tissue. The bodies which secondarily become fixed to the synovial membrane may undergo ossification.

The number of detached bodies varies between one and more than a thousand. This observation made *Brenckmann* distinguish between 2 forms of articular chondromatosis, viz. a traumatic and an atraumatic form. In the traumatic form there occurs only a transitory disturbance of the equilibrium in the synovia, and consequently only a small number of bodies are

formed. Reversely the atraumatic form is associated with disturbance of the equilibrium of longer duration, resulting in development of a large number of bodies (1200 or more).

The nodules may thus be situated either as detached bodies in the joint or fixed to the capsule or the bone. When present in great numbers they will give rise to usure of bone and cartilage. They may even penetrate through the latter and come to be situated outside the joint (*Burckhardt* 1932, *Lindén* 1934, and *Radner* 1941).

Burckhardt 1932 states, as a radiographic differentiation from the joint mice in arthrosis deformans, that the chondromatosis joint is normal, except for the bodies, whereas the arthrosis joint always is pathologically changed. Arthrosis deformans may develop secondarily at advanced stages of chondromatosis (*Brenckmann* 1927 and *Burckhardt* 1932). In such cases it may be impossible to make a differential diagnosis.

b. Articular osteomatosis:

Articular osteomatosis is another benign disease by no means rare, but little known, however. The most frequent mistaken diagnosis is one of arthrosis deformans. Articular osteomatosis is separated out as an independent disease by *Kienböck* in 1924 (*Kienböck* 1938).

Articular osteomatosis is a benign tumour form, which may be situated in any part of the joint, viz. the fibrous capsule, the synovial membrane, and the superficial part of the articular bone. The bony tissue developed consists of spongy bony tissue covered by a thin compact layer.

A distinction is made between fixed bone osteomas and movable capsule osteomas. The fixed osteomas may present themselves either as diffuse hyperosteoses or as pointed marginal exostoses. The latter are apt to break off, and often they remain detached. The capsule osteomas may be intra-, inter-, or extracapsular. Moreover, they may be torn off and become joint mice. The osseous form, the capsular form or both forms may be present simultaneously in one patient.

The osteomas may be small, and are then generally multiple, or large, and are then generally solitary. Yet, small solitary capsule osteomas may very well be found.

The disease affects chiefly adult individuals of both sexes

in a good general state of health. The mobility of the joint is in the general preserved. The joints of knee and elbow are the sites of choice, but also ankle joints, tarsal joint (notably the talonavicular joint), and phalangeal joints have been seen to be affected. Most often only one joint is affected, more rarely two (then generally symmetrical), and very rarely more joints.

Articular osteomatosis may be associated with articular chondromatosis.

4. *Osteochondrosis dissecans*.

The following comprehensive remarks on osteochondrosis dissecans are taken mainly from *Nielsen's* monograph 1933. Osteochondrosis dissecans manifests itself as a well-defined partial subchondral lesion of certain articular surfaces. The process is at first only subchondral, but later a minor part of the hyaline cartilage is involved, too. In most cases the subchondral seat of the process with the overlying hyaline cartilage is chipped off to make a joint mouse.

The sites of choice are, according to *Hellström & Östling* 1934, knee joint (63 per cent) and elbow joint (33 per cent). The authors state, however, that in other statistics the elbow may be found to be affected more frequently than the knee. Other articular surfaces may be affected. Thus, as regards the foot, cases have been reported of lesion of the talocrural joint (*Stevenson* 1925, *Wolff* 1925, *Läwen* 1929, *Puhl & Lindemann* 1938, and *Rasmussen* 1945), the cuneometatarsal I joint (*Hertz* 1938), and the posterior talocalcaneal joint (*Schnarberth* 1939).

The defect in the articular surface may to a greater or smaller extent be compensated for. The bony tissue is replaced by a somewhat dense, but otherwise normal spongy tissue, but with no articular lamellae against the surface, while the hyaline cartilage is replaced by connective tissue cartilage.

The joint mouse consists of a small piece of bony tissue with overlying normal hyaline cartilage. Later the osseous surface is covered by connective tissue cartilage. This process has probably started already before the mouse has been completely separated off (*Burckhardt* 1932). The mouse increases somewhat in size and absorbs calcium the first few years after it has been separated off. After that it remains stationary.

Microscopically the mouse is seen to consist of ordinary bony tissue intermixed with necrotic tissue, hyaline cartilage, and connective tissue cartilage. In the great majority of cases there are found only one or a few mice. The detached mice may secondarily become adherent to the joint capsule.

In rarer cases no mouse is separated off. The affected bone area heals up again, hardly leaving any traces. *Wiberg* 1941 reports 6 cases in which the lesion was seen radiographically (and clinically) to have been cured.

Radiographically (*Nielsen* 1933, *Hellström & Östling* 1934, and *Schinz, Baensch & Friedl* 1939) osteochondrosis dissecans is seen as a well-defined rarefaction in the bone, conditioned in some measure by a condensation of the adjacent bony tissue. Later a well-defined detached bone (the future mouse) is seen within the injured area, surrounded by a clear ring. If the mouse is separated off one finds a more or less deep defect in the articular cartilage, which at a later stage is filled up, to disappear entirely, if the best happens. *Leriche, Jung, & Berthel* 1939 submitted 10 patients operated on (in the knee) to radiographic follow-up examination from a few months to 10 years after the operation. Independently of the time, 5 patients presented nothing abnormal. Other investigators find more often slightly spotted markings or a ring-shaped shadow corresponding to the site of the mouse. In addition the bone is generally somewhat flattened in the area concerned, and a light arthrosis deformans may develop in the joint.

The mouse may often be difficult to recognize radiographically immediately after it has been separated off. But after a few years it becomes easily recognizable as a well-defined detached intra-articular bone.

Nothing certain is known of the cause of this lesion. The disease must be reckoned to begin about the age of 14 or 15, and to run a symptom-free course in ab. half of the cases. In the other half the symptoms occur rather promptly. They may abate after some time, only to recur with renewed intensity because of the mouse.

The lesion occurs chiefly in men (notably manual labourers). *Nielsen* found 41 cases among 1000 normal men chosen at random. Among 133 cases giving rise to symptoms he found the right foot affected in 59 per cent, the left in 15 per cent, and

both in 26 per cent. Moreover, he observed a certain familial predisposition.

These facts induce many investigators to regard the disease as dependent on a certain constitutional predisposition (probably on a hereditary basis) in connection with processes corresponding to those seen in aseptic necroses. *Burckhardt* 1932 holds that the occurrence of the disease always depends on traumatic-mechanical factors, but the trauma is not always clinically conspicuous.

Ribbing 1944 presents a well-founded aetiology. First, by radiographs of 193 boys and 198 girls between the ages of 0 and 10 years, he shows that inconstant accessory bone centres may develop (most often in boys) superficially in the distal femoral epiphysis and the epiphysis for the head of the humerus in areas corresponding exactly to the sites of osteochondrosis dissecans. Histological serial-section analyses show that such a centre is isolated from the proper epiphyseal centre, and that it has only a single source of vascular supply. *Ribbing* takes this subchondral centre to constitute a *locus minoris resistentiae* and, therefore, liable to be torn off, merely by the physiological minor traumas to which the joint is exposed. Because of the consequent lack of nutrition an aseptic necrotic process takes place here, which will finally lead to complete detachment. The occurrence of osteochondrosis dissecans is thus due to the interaction of a constitutional (probably hereditary) factor, i. e. the accessory bone centre, and a mechanical factor, i. e. the physiological articular function, possibly in connection with minor traumas.

C. LESIONS AFFECTING THE SOFT TISSUES

1. *Traumatic Soft Tissue Lesions.*

Any traumatic soft tissue lesion may lead to the formation of bone. According to *Leriche & Policard* 1926 and *Leriche* 1939 this can be explained as being due to a traumatically determined development at the site of lesion of young unspecific oedematous connective tissue of the embryonal type in connection with an active vasodilatation released by the trauma, which leads to rarefaction of the adjacent bone. According to *Levander* 1934, 1940, and 1941 the formation of bone is due to an

interaction of the unspecific mesenchymal tissue developed at the site of lesion and activating, bone-forming substance liberated from the blood at the site of lesion.

It is worth noting that the formation of bone takes place without simultaneous lesion of the osseous system, a fact which has been stressed by *Leriche & Jung* 1940, also for fractures. They state that the formation of bone is determined exclusively by the trauma, and not by the presence of the fracture.

Any soft tissue lesion, due, for instance, to contusion (including operation wounds), distortion, and dislocation, may thus give rise to circumscribed new bone formation (cf. *myositis ossificans circumscripta*).

A case published by *Bier* 1923 is a droll example of soft tissue lesion leading to new bone formation: A man, aged 54, developed a subcutaneous haematoma in connection with an ordinary venous puncture in the elbow bend. Most of the haematoma was resorbed again, leaving only a small hard area. About 6 months later the patient had developed ankylosis in the elbow with demonstrable bone formation round the joint and half-way up the upper arm. The bone was situated both subcutaneously and intramuscularly.

2. *Myositis Ossificans*.

Myositis ossificans manifests itself in 2 essentially different forms, the circumscribed and the progressive. With a view to the accessory bones it is only the circumscribed form which is of interest. This form, which may be found at all ages and in both sexes, shows bone formation in a single circumscribed area, generally on the extremities. Microscopically there is seen hyaline cartilage and fibrous cartilage in addition to bony and osteoid tissue.

The aetiology of the circumscribed form is somewhat doubtful, but in the great majority of the cases a well-pronounced, locally acting factor, most often a trauma, seems to be the releasing cause. (As for details and literature reference may be made to *Povlsen* 1935).

3. *Calcinosis*.

Calcium is deposited in the tissues, particularly so round the joints, both in the circumscribed and the universal form of

calcinosis. In the circumscribed form the calcium deposits are generally well-defined, up to pea-sized formations, while in the universal form they have a more diffuse character, sometimes occurring as long bands. The lesion may be found in both sexes and at any age, the circumscribed form, however, particularly among women after the menopausal age (*Schinz, Baensch, & Friedl* 1939, *Kalbak* 1940, *Bäfverstedt* 1941, and *Pedersen* 1943). The pathogenesis is unknown. The calcium metabolism is normal.

With a view to the accessory bones it is the circumscribed form with its few, well-defined calcium deposits which are of interest. This form is, moreover, generally localized in the distal extremital parts. Calcium deposits are found in skin, subcutaneous tissue, muscles, nerves, and the loose connective tissue. Genuine bone formations are found mentioned in a small proportion of the calcinosis cases (*Bäfverstedt* 1941 and *Pedersen* 1943).

Sandström 1938 mentions a special form of calcinosis called by him *peritendinitis calcarea*, by which, despite the name, is understood calcium deposits in tendons, peritendinous tissue, and joint capsules. In rare cases bony tissue is said to develop as well (*Sandström*).

4. *Osteoma Cutis.*

Cutaneous osteoma is due to an isolated bone formation in the corium. A distinction is made between a congenital form (where no releasing factor can be found) and an acquisite form [developed in consequence of inflammation (e. g. acne), a trauma (including operation wounds), or the like]. Microscopically the new-formed bone presents a typical bony structure, but no deposits of cartilage or calcium have been found (*Pirilä* 1941).

5. *Chondromatosis.*

Articular chondromatosis has been mentioned among the lesions of the articular apparatus. However, not only the articular apparatus, but also bursae and tendon sheaths may present chondromatosis, either isolated or with concurrent affection of one or more joints (*Panner* 1926, *Brenckmann* 1927, and *Burckhardt* 1932).

6. *Vascular Calcifications.*

a. Arteriosclerosis:

may occasionally lead to circumscribed calcifications in a single or but a few places. They are, however, rarely well-defined. If such a place happens to correspond to the site of an accessory bone the two conditions may easily be mixed up. One of my own cases illustrates this fact (p. 29, Fig. 10).

b. Phleboliths:

may, though rarely indeed, be found in the veins of the foot (*Haenisch, Holthusen, & Liechti* 1940).

7. *Dystrophic Calcification and Ossification.*

Any necrobiotic and necrotic tissue is apt to absorb calcium, the so-called dystrophic calcification (*Barr* 1932), whereas ossification is of rarer occurrence. Small limited necrotic foci may give rise to formations resembling accessory bones.

8. *Calcified Parasites.*

In rare cases there may be found calcified *Cysticerci*, *Trichinae*, and *Filariae* in the foot (*Haenisch, Holthusen, & Liechti* 1940 and *Schinz, Baensch, & Friedl* 1939).

9. *Foreign Bodies.*

Foreign bodies should also just be mentioned for completeness' sake.

SUMMARY

Introduction: The object of the present work is partly to point out the great variety and frequency of accessory bones in the foot, and partly to contribute to a solution of the question of the genesis of the accessory bones, notably the question whether or not these bones should be regarded as phylogenetic formations.

Chapter 1: The work is based on the following definition of accessory bones: *Accessory bones are all inconstant, independent, well-defined bones — in an otherwise normally developed foot — the existence of which is not due to a recent minor fracture or other definitely pathological condition, no matter whether these bones bear no, or a less or more intimate relationship to the constant bones, or entirely replace them because of a division of the latter into several segments.*

It is a very wide-ranging definition, but, as will be seen from the present work, this cannot be otherwise.

Next follows a Table of the 35 accessory bones mentioned here, in which the frequency of occurrence is indicated. Finally a summary description is given of the site of each of them, accompanied by a radiograph and/or a drawing after anatomical preparations. It is pointed out that this description does not include all the accessory bones that may be found in the foot.

Chapter 2: A study aiming at elucidating the question of the genesis of the accessory bones requires a systematic histo-embryological serial-section analysis with examination of each individual section of a large number of feet from embryos of different ages, because in numerous cases the ontogenesis is a recapitulation of the phylogenesis. A material of this kind, of which none is available in the literature, is presented here in chapter 2, comprising 508 paired feet from 254 embryos between

the ages of 6 and 27 weeks (supplemented by a few investigations of 25 feet from full-term, still-born children).

All these embryonic feet were cut in serial sections, and each section was mounted, stained, and histologically examined (a total of well over 300.000). The skeleton of the foot is not yet laid down in embryos from 6 to 6½ weeks old (copulation age). There is found only a homogeneous mesenchymal substance, which allows of no differentiation of the individual future bones, not even of a distinction between future bony, tendinous, and muscular tissues. In older embryos the individual tarsal and metatarsal primordia begin to be distinguishable as prochondral nests. In embryos older than 8 weeks (menstruation age) the tarsal and metatarsal elements become cartilaginous, between 9 and 11 weeks of age also the phalanges, and finally between the ages of 11 and 12 weeks the 2 constant sesamoid bones of the big toe.

We do not know whether a primordial bone develops from a number of prochondral nests corresponding to the evolution of the bone in question from the elements of the primitive tetrapod foot, or whether the number of nests is independent thereof, even perhaps varies from one individual to the other. Moreover, we are unable to discern lines of division between the individual nests and between groups of several nests. It, therefore, seems justifiable to make the following requirement: *Only if an accessory bone has been demonstrated as an independent hyaline cartilage formation can it be said for certain to have been laid down independently.*

Hence, the embryological investigations aiming at elucidating whether the accessory bones are present as independent elements at the hyaline cartilage stage were made on embryos older than 8 weeks (menstruation age).

500 feet (250 pairs) have been obtained for this investigation. The following accessory bones are found as independent hyaline-cartilaginous elements in the present material (the figures in parentheses indicate the percentage frequencies, the former for pairs of feet, and the latter for number of feet):

- calcaneus accessorius* (0.8 and 0.6),
- os cuneiforme I bipartitum* (2.4 and 2.4),
- os intermetatarsale I* (8.0 and 6.8),
- os interphalangeale* (2.7 and 1.9),

os paracuneiforme (13.2 and 13.2),
os peroneum (0.4 and 0.4),
os sesamoideum metatarsophalangeale II (4.3 and 4.0),
os sesamoideum metatarsophalangeale III (1.1 and 0.53),
os sesamoideum metatarsophalangeale IV (2.7 and 2.7).
os sesamoideum metatarsophalangeale V (26.2 and 26.2),
os sesamoideum interphalangeale dig. I (57.8 and 56.0),
os sesamoideum interphalangeale proximale dig. V (9.6 and 9.1).

os sesamoideum partitum interphalangeale dig. I (2.7 and 1.8),
os subfibulare (0.4 and 0.2),
os tibiale (7.6 and 6.4).

My embryological investigations give the following results: 11 of the 35 accessory bones mentioned in the present work (31.5 per cent) are found as independent hyaline-cartilaginous elements. The percentage frequencies for these 11 is, however, not the same as for the corresponding bones in adults. Nearly 80 per cent of the embryos present accessory bones preformed in hyaline cartilage. These are distributed as follows: nearly 10 per cent exclusively in and about the tarsus, well over 45 per cent about the metatarsophalangeal and the interphalangeal joints, and 22 per cent of both categories.

Moreover, my systematic serial-section analyses show that only by examining each section one can be quite certain that a cartilaginous element really is independent. The investigation is of no value if it is based on individual sections only. Instances are given of this fact.

Finally I made other observations, which, however, have no bearing on the present investigation. Thus, I found synchronosis between 2 constant, normally independent cartilaginous elements, congenital crural defect, and other crural anomalies. Furthermore I fixed the time of beginning ossification for various bones of the foot (with mention of a practically unknown perichondrial calcanean centre), and showed that male abortions are more frequent than female.

Chapter 3: To be able to give an opinion as to whether the accessory bones found as independent elements already at the hyaline cartilage stage are phylogenetic or not it is necessary to have a knowledge of the constructions of the feet of other

vertebrates, in particular the embryological constructions. Various investigations have been published in the literature of embryos from all mammalian orders as well as birds, reptiles, and amphibians. A number of such investigations are reported in this chapter.

Chapter 4. Discussion I: The question whether an accessory bone in the human foot, demonstrated to have been preformed in hyaline cartilage, really is of phylogenetic origin cannot be answered on the basis of a comparative embryological vertebrate material alone, but it is necessary also to know how the primitive tetrapod foot is constructed. The results of some recent investigations into the construction are reported here.

The question of the phylogenetic genesis of the accessory bones found in the feet of adult humans is discussed on the bases of: 1) demonstration of independent hyaline-cartilaginous primordia of certain accessory bones in embryos, 2) embryological vertebrate material for comparison, and 3) a knowledge of the construction of the primitive tetrapod foot.

The following accessory bones should — according to statistical calculations — be demonstrable in my material, in case they are preformed in hyaline cartilage as independent elements: *calcaneus secundarius*, *os intermetatarsale I*, *os peroneum*, *os sesamoideum interphalangeale*, *os sesamoideum metatarsophalangeale*, *os sesamoideum partitum interphalangeale* and *metatarsophalangeale*, *os tibiale*, and *os trigonum*.

These 8 accessory bones are dealt with separately.

Calcaneus secundarius: I have not found this bone laid down in embryos.

Os intermetatarsale I: is found in embryos with a frequency corresponding to that in adults.

Os peroneum: I have found it in embryos, but with a frequency which is out of all proportion to that demonstrated in adults (0.4 per cent against 6 to 8 per cent).

Os sesamoideum interphalangeale: found in embryos with the same frequency as in adults.

Os sesamoideum metatarsophalangeale: the same.

Os sesamoideum partitum: I found the interphalangeal sesamoid bone divided 6 times in embryos, but never so the metatarsophalangeal, though its frequency in adults is up to 30 per cent.

Os tibiale: found in embryos with the same frequency as in adults.

Os trigonum: is never found in embryos, despite its frequent occurrence in adults.

Of these 8 accessory bones only 1 can be explained on a phylogenetic basis. This is the *os tibiale*, which is found both in other vertebrates (in embryos as well as in adult animals) and in the primitive tetrapod foot. It corresponds to the element called *tibiale*.

The *interphalangeal* and *metatarsophalangeal* *sesamoid* bones have been found with certainty only within the class of mammals. Hence they may be regarded as neogenetic formations, i. e. formations developed at a later stage of the evolution.

The *os intermetatarsale I* has been found only in man. Since it has not been demonstrated embryologically in other vertebrates, and has not been found in the primitive tetrapod foot either, it must for the present be regarded as a congenital anomaly.

The *os peroneum* and the *os sesamoideum bipartitum* occur with far higher percentage frequencies in adults than those demonstrated in embryos. In adults they have, moreover, been found only among the most highly developed mammals. Accordingly these bones are not of phylogenetic origin; and, because of their rare occurrence in embryos, they cannot generally be regarded as congenital formations either.

Finally, neither the *calcaneus secundarius* nor the *os trigonum* have been found in embryos.

In addition to the above accessory bones I have found also others preformed in hyaline cartilage, bones which I could not expect to find, on account of their rare occurrence in adults. These latter accessory bones are the following: *calcaneus accessorius*, *os cuneiforme I bipartitum*, *os interphalangeale*, *os paracuneiforme*, and *os subfibulare*. They are dealt with separately.

Calcaneus accessorius: found 3 times in embryos. The frequency in adults has not been indicated, but it is at any rate a fairly rare phenomenon.

Os cuneiforme I bipartitum: is found in embryos with a higher percentage frequency than the corresponding findings in adults (2.5 per cent against 0.5 per cent).

Os interphalangeale: is found 7 times in embryos. The frequency in adults is indicated nowhere in the literature.

Os paracuneiforme: is found in 13 per cent of the embryos, a frequency which is out of all proportion to that seen in adults, where the bone is an extremely rare phenomenon.

Os subfibulare: is perhaps seen in one embryo. In adults the bone is likewise of rare occurrence.

Of these 5 accessory bones only 1 can be accounted for on a phylogenetic basis. This is the *os paracuneiforme*, which is found in other vertebrates (both in embryos and in adult animals) as well as in the primitive tetrapod foot. In the latter it corresponds either to the centrale prehallucis or the tarsale prehallucis. That I found the primordium so much more frequently in embryos than the corresponding bone has been observed in adults is probably due to the fact that the cartilaginous primordium either disappears again or does not ossify.

The *calcaneus accessorius*, the *os interphalangeale*, and the *os subfibulare* are found only in man. They have not been observed in the embryos of other vertebrates. Neither are they present in the primitive tetrapod foot. These accessory bones may, therefore, be regarded as congenital anomalies.

The *os cuneiforme I bipartitum* has been demonstrated only in human embryos. Besides in adult humans, it is said to have been found a single time in an adult possum and an adult tree porcupine; but never in any other vertebrates. Neither is it present in the primitive tetrapod foot. Hence its presence cannot be explained on a phylogenetic basis. I do not know how to explain it, but presumably it is a congenital anomaly.

Finally there is reason to mention that other writers claim to have found the *os trigonum* and the *os Vesalianum* as independent hyaline-cartilaginous elements in human embryos.

Os trigonum: As already mentioned, I have never in human embryos found this bone as an independent element at the hyaline cartilage stage, although it is seen in 7 to 10 per cent of adult humans. This alone makes me call in question other writers' observations of an independent primordial *os trigonum* in human embryos. A further review of their investigations also shows that they are not proof against criticism. In my opinion the *os trigonum* has not been demonstrated in the human embryo, and there is found no element in the primitive tetrapod foot corresponding to this bone.

Os Vesalianum: The bone was not observed in my embryo-

logical material. This is only what one should expect, since it is an extremely rare phenomenon in adults. One writer reports, however, a finding in a new-born — unfortunately deformed — child. It seems to me justifiable to conclude from the comparative embryological investigations within the vertebrates and the construction of the primitive tetrapod foot that the *os Vesalianum* is of phylogenetic origin, traceable to the tarsale 5 (possibly the tarsale 6 = *postminimus*).

Result: Independent accessory bones preformed in hyaline cartilage in the human embryo can, according to circumstances, be explained as phylogenetic formations, neogenetic formations, or accidental anomalies.

Chapter 4. Discussion II: It has been maintained by certain writers that the presence of inconstant ossification centres in one cartilaginous primordium in many cases are suggestive of original independence of the part concerned. In other words, if there is found an independent ossification centre in the place corresponding to an accessory bone, then a failing embryological demonstration of a hyaline-cartilaginous primordium of the accessory bone does not necessarily preclude this bone from having originally been independent (whether of phylogenetic, neogenetic, or anomalous origin).

To be able to decide whether the accessory bones may be conditioned by the presence of inconstant ossification centres it is necessary to collate all that is known about the presence of inconstant ossification centres in the foot. This has been done on the basis of the literature, and statements concerning a number of mammals have been added as a supplement.

By comparing the sites of the different accessory bones with those of the inconstant ossification centres it is seen that the following accessory bones may correspond to inconstant ossification centres, and, therefore, be explained by these: *calcaneus accessorius*, *os cuneiforme I bipartitum*, *os cuneometatarsale I plantare*, *os naviculare bipartitum*, *os sesamoideum partitum metatarsophalangeale*, *os subfibulare*, *os subtibiale*, *os sustentaculi proprium*, *os talonaviculare dorsale*, *os tibiale*, *os trigonum*, *os tuberis calcanei*, and *os Vesalianum*.

Of these accessory bones the following 4 are situated so as possibly to correspond to elements in the primitive tetrapod

foot: *os naviculare bipartitum*, *os subtibiale*, *os tibiale*, and *os Vesalianum*. This again means that if the existence of the 4 accessory bones is due to the presence of inconstant ossification centres, these centres may be explained on a phylogenetic basis.

As for the remaining 9 accessory bones it can only be said that if they owe their existence to the presence of inconstant ossification centres, these centres may either be due to original, independent hyaline-cartilaginous primordia (neogenetic or anomalous) or be secondary ossification centres developed from an unknown cause, independently of previously present primordia.

A condition that inconstant ossification centres may explain the presence of accessory bones is that these centres do not always fuse to the remaining primordial bone. Here we come to the question of persisting epiphyses and coalescence. It is evidenced on the basis of the literature that the epiphyseal development is the normal for the inconstant ossification centre, leading to synostosis simultaneously with the conclusion of the growth, while the development of coalescence is pathological, and often does not lead to synostosis. The coalescence must be ascribed to regressive changes in the cartilage, caused by unphysiological overcharging.

Result: Inconstant ossification centres must be supposed sometimes to be the cause of the presence of accessory bones. The inconstant ossification centres must in certain cases be regarded as the last remains of originally independent cartilaginous primordia, whether these primordia be of phylogenetic, neogenetic, or anomalous origin. In other cases these centres must be regarded as phenomena developed independently of previously present primordia.

Chapter 4. Discussion III: Not all accessory bones can be explained as having developed from an independent element preformed in hyaline cartilage or an inconstant ossification centre. The *os peroneum*, for instance, cannot yet be accounted for to satisfaction. The results of recent thorough investigations published in the literature seem, however, to prove that the *os peroneum* is a tendon bone, i. e. a secondary bone developed postnatally in response to localized irritants acting from without.

Similar investigations have been made with regard to the *os tibiale*, and with the same results.

Result: Certain accessory bones can be explained as tendon bones, i. e. bones developed postnatally in response to irritants acting from without.

Chapter 4. Discussion IV: It is an established fact that various pathological conditions may give rise to detached independent bones (cf. osteochondrosis dissecans or chondromatosis). The independent bones thus developed are not included in my definition of accessory bones. There is, however, hardly any doubt that many accessory bones owe their existence to pathological conditions the natures of which cannot be definitely recognized (in the first instance old pseudarthrotic minor fractures). It is, therefore, only reasonable that the present work should end with an account of the lesions which may give rise to the formation of detached independent bones. I have divided these lesions in 3 groups, namely in lesions affecting A) the osseous system, B) the articular apparatus, and C) the soft tissues. The lesions belonging to each of these 3 groups are mentioned:

ad A: fractures, infections, aseptic bone necroses, and circumscribed bone condensations.

ad B: fractures, arthroses, arthromas, osteochondrosis dissecans.

ad C: traumatic soft tissue lesions, myositis ossificans, calcinosis, osteoma cutis, chondromatosis, vascular calcifications, dystrophic calcifications and ossifications, calcified parasites, and foreign bodies.

Result: Accessory bones may owe their existence to non-recognized pathological conditions.

CONCLUSIONS

An accessory bone may be due to:

- 1. An independent hyaline-cartilaginous primordium, which may be of phylogenetic, neogenetic, or anomalous origin.*
- 2. A process of coalescence for an inconstant ossification centre. This centre may again either be derived from an originally independent element preformed in hyaline cartilage (phylogenetic, neogenetic, or anomalous) or be a secondary ossification centre of unknown origin, but developed independently of previous independence.*
- 3. A tendon bone, i. e. a postnatal formation developed on account of local irritants acting from without.*
- 4. A non-recognized pathological lesion, in the first instance an old pseudarthrosic minor fracture.*

Finally there is reason to emphasize the fact that one and the same type of accessory bone need not have the same genesis in different individuals.

SUMMARY IN DANISH

Indledning: Formaålet med dette arbejde er, dels at paapege fodens accessoriske knoglers mangfoldighed og hyppighed og dels give et bidrag til spørgsmaalet om de accessoriske knoglers genese, specielt om de er at betragte som phylogenetiske dannelser eller ej.

Første kapitel: Arbejdet er bygget over følgende definition af accessoriske knogler: *Ved accessoriske knogler forstaas alle — i en iøvrigt normal udvoxet fod — tilstedeværende inkonstante, selvstændige, velaftgrænsede knogler, der ikke skyldes en nærværende frisk detaillefractur eller anden sikker patologisk lidelse, og det hvad enten disse knogler er uden, i mindre eller mere intim relation til de konstante knogler eller ganske erstatter de konstante paa grund af disses deling i flere stykker.*

Som det ses, er det en vid definition, men at det ikke kan være anderledes, viser det foreliggende arbejde.

Herefter følger et skema over de i dette arbejde omtalte 35 accessoriske knogler, over deres hyppighed og endelig gives en summarisk beskrivelse af deres beliggenhed, ledsaget af røntgenfotografier eller billeder efter anatomiske præparater. Det pointeres sluttelig, at antallet af accessoriske knogler i foden ikke maa betragtes som afsluttet med de her omtalte accessoriske knogler.

Andet kapitel: For at komme til klarhed over de accessoriske knoglers genese, er en systematisk histo-embryologisk seriesnit-undersøgelse, med undersøgelse af hvert enkelt snit paa et stort antal embryonfodder i forskellige alderstrin, absolut nødvendig, idet ontogenesen i mangfoldige tilfælde giver en rekapitulation af phylogenesen. Et saadant materiale mangler hidtil i litteraturen. Derfor fremlægges i dette kapitel et saadant materiale bestaaende af 508 parrede fodder fra 254 embryoner

i alderen 6—27 uger (suppleret med enkelte undersøgelser paa 25 fødder fra fuldbaarne, dødfødte børn).

Samtlige disse embryonfødder er skaaret i seriesnit, hvert enkelt snit er opklæbet, farvet og histologisk undersøgt (ialt godt 300.000). Hos 6—6½ uger gamle (copulation age) embryoner er fodskelettet endnu ikke anlagt, der findes kun en ensartet mesenchymmasse, der ikke tillader nogen uddifferentiering af de enkelte senere knogleanlæg, ja end ikke adskillelse mellem de senere knogle-, sene- eller muskelvæv. Hos ældre embryoner begynder de enkelte tarsal- og metatarsalanlæg at uddifferentieres som forbruskreder, men først hos embryoner ældre end 8 uger (menstruation age), er tarsal- og metatarsalanlæggene bruskede, phalanges først hos 9—11 uger gamle embryoner og endelig storetaens 2 konstante sesamben først hos 11—12 uger gamle embryoner.

Da man ikke ved, om et knogleanlæg opstaar udfra et antal forbruskreder svarende til den paagældende knogles opbygning af primitive tetrapodefods elementer, eller om antallet af reder er ganske uafhængigt heraf, ja maaske endog varierende fra individ til individ, og da endvidere skarpe grænser mellem de enkelte forbruskreder eller mellem grupper af flere forbruskreder mangler, maa det være rimeligt at stille følgende krav: *Kun dersom en senere accessorisk knogle er paavist som selvstændigt hyalinbrusk anlæg, kan man sikkert sige, at den er selvstændigt anlagt.*

Derfor er de embryologiske undersøgelser, der skal give oplysninger om de accessoriske knoglers eventuelle selvstændige hyalinbruskanlæg gjort paa embryoner ældre end 8 uger (menstruation age). Af fødder fra saadanne embryoner haves 500 (parrede). I dette materiale er følgende accessoriske knogler fundet som selvstændige hyalinbruskanlæg og med saa og saa stor hyppighed i procent (det første tal beregnet paa fodpar, det andet paa antal fødder):

calcaneus accessorius (0,8—0,6).

os cuneiforme I bipartitum (2,4—2,4).

os intermetatarsale I (8,0—6,8).

os interphalangeale (2,7—1,9).

os paracuneiforme (13,2—13,2).

os peroneum (0,4—0,4).

os sesamoideum metatarso-phalangeale II (4,3—4,0).

- os sesamoideum metatarso-phalangeale III* (1,1—0,53).
- os sesamoideum metatarso-phalangeale IV* (2,7—2,7).
- os sesamoideum metatarso-phalangeale V* (26,2—26,2).
- os sesamoideum interphalangeale dig. I* (57,8—56,0).
- os sesamoideum interphalangeale proximale dig. V* (9,6-9,1).
- os sesamoideum partitum interphalangeale dig. I* (2,7—1,8).
- os subfibulare* (0,4—0,2).
- os tibiale* (7,6—6,4).

Samler man resultatet af mine embryologiske undersøgelser, finder man først, at 11 af de i dette arbejde omtalte 35 accessoriske knogler er fundet hyalinbruskpræformerede, i. e. 31,5 %, omend procenten for disse 11 ikke er den samme som for de tilsvarende hos voksne. Dernæst viser det sig, at der hos næsten 80 % af embryonerne findes hyalinbruskpræformerede accessoriske knogler fordelt paa næsten 10 % udelukkende om og i tarsus, godt 45 % omkring de metatarso-phalangeale og interphalangeale led og 22 % af begge slags anlæg.

Endvidere viser mine systematiske seriesnit-undersøgelser, at kun ved undersøgelse af hvert enkelt snit faar man sikkerhed for, at et bruskelement virkelig er selvstændigt. Undersøges kun enkelte snit har undersøgelsen ingen værdi; eksempler herpaa gives.

Endelig har jeg gjort andre — dette arbejde uvedkommende — fund, saa som paavist synchondrose mellem 2 normalt konstante selvstændige bruskelementer, fundet congenit crusdefect, fastlagt tidspunktet for ossificationens indsættelse for en række af fodens knogler (med omtale af en saa godt som ukendt perichondral calcaneuskærne) og vist, at ♂-aborter er hyppigere end ♀-aborter.

Tredje kapitel: For nu at kunne udtale sig om, hvorvidt de saaledes fundne hyalinbruskpræformerede selvstændige accessoriske knogler er phylogenetiske eller ej, er det nødvendigt ogsaa at have kendskab til andre hvirveldyrfødders opbygning, specielt deres embryologiske. Fra literaturen er samlet en række saadanne fund fra saavel samtlige pattedyrordner, som fra fugle, krybdyr og padder.

Fjerde kapitel, diskussion I: For at kunne afgøre om et hos mennesket paavist selvstændigt hyalinbruskanlæg for en acces-

sortisk knogle virkelig er phylogenetisk, er det imidlertid ikke nok at have et sammenlignende embryologisk hvirveldyr-materiale, man maa ogsaa kende den primitive tetrapodefods opbygning. Resultatet af nogle af de sidste aars undersøgelser herover fremlægges.

Med disse kort paa haanden: 1) paavisning af visse accessoriske knoglers selvstændige hyalinbruskanlæg hos embryoner, 2) kendskab til et sammenlignende embryologisk hvirveldyr-materiale og 3) viden om den primitive tetrapodefods opbygning, er nu spørgsmaalet om den eventuelle phylogenetiske genese af de i voksne menneskelige fødder fundne accessoriske knogler taget op.

Efter de accessoriske knoglers hyppighed hos voksne mennesker, burde jeg — efter statistiske beregninger — i mit materiale have paavist følgende — saafremt de er selvstændige hyalinbruskanlæg: *calcaneus secundarius*, *os intermetatarsale I*, *os peroneum*, *os sesamoideum interphalangeale*, *os sesamoideum metatarso-phalangeale*, *os sesamoideum paritum interphalangeale* og *metatarsophalangeale*, *os tibiale* og *os trigonum*. Disse 8 accessoriske knogler skal nærmere gennemgaa:

Calcaneus secundarius: jeg har overhovedet ikke fundet det embryologisk.

Os intermetatarsale I: det er fundet embryologisk med tilsvarende hyppighed som hos voksne.

Os peroneum: jeg har fundet det embryologisk, men med en hyppighed, der staar i skærende misforhold til den hos voksne paaviste hyppighed (0,4 % mod c. 6—8 %).

Os sesamoideum interphalangeale: det er fundet embryologisk med tilsvarende hyppighed som hos voksne.

Os sesamoideum metatarso-phalangeale: herfor gælder det samme.

Os sesamoideum paritum: de interphalangeale har jeg 6 gange fundet embryologisk, de metatarso-phalangeale derimod aldrig, skønt de findes hos voksne med op til 30 %'s hyppighed.

Os tibiale: det er fundet embryologisk med tilsvarende hyppighed som hos voksne.

Os trigonum: jeg har overhovedet aldrig fundet det embryologisk trods dets hyppighed hos voksne.

Af disse 8 accessoriske knogler, er der kun 1, der kan phylogenetisk forklares, det er *os tibiale*, idet det findes saavel hos

andre hvirveldyr (baade embryologisk og hos udvoxede) som i den primitive tetrapodefod; det svarer her til elementet: tibiale.

De *interphalangeale* og *metatarso-phalangeale* sesamben er kun sikkert fundet indenfor pattedyrenes klasse, de kan derfor betragtes som neogenetiske dannelser, i. e. dannelser opstaaet paa et senere trin i udviklingen.

Os intermetatarsale I er kun fundet hos mennesket; da det ikke er paavist embryologisk hos andre hvirveldyr, og ej heller findes i den primitive tetrapodefod, maa det indtil videre betragtes som en medfødt anomali.

Os peroneum og *os sesamoideum partitum* er ikke paa langt nær fundet embryologisk med den til voxne svarende hyppighed; endvidere er de hos voxne kun fundet indenfor de højst udviklede pattedyr; phylogenetiske er disse accessoriske knogler saaledes i hvert fald ikke, og paa grund af de sjældne embryologiske fund, kan de heller ikke almindeligvis være congenite dannelser.

Endelig er hverken *calcaneus secundarius* eller *os trigonum* embryologisk fundet.

Foruden de her omtalte accessoriske knogler, har jeg imidlertid ogsaa fundet andre accessoriske knogler, som hyalinbruskanlæg, knogler som jeg efter deres sjældenhed hos voxne ikke kunde forvente at finde. Disse accessoriske knogler er: *calcaneus accessorius*, *os cuneiforme I bipartitum*, *os interphalangeale*, *os paracuneiforme* og *os subfibulare*. De skal nærmere gennemgaa:

Calcaneus accessorius har jeg fundet embryologisk 3 gange. hyppigheden er ikke angivet hos voxne, men almindelig er den i hvert fald ikke.

Os cuneiforme I bipartitum har jeg fundet embryologisk med en større hyppighed end det tilsvarende fund hos voxne (2,5 % mod 0,5 %).

Os interphalangeale har jeg embryologisk fundet 7 gange, hyppigheden hos voxne er ikke angivet noget steds.

Os paracuneiforme har jeg embryologisk fundet i 13 %, hvad der staar i skarpt misforhold til, at knoglen hos voxne er saare, saare sjælden.

Os subfibulare har jeg maaske fundet embryologisk 1 enkelt gang; hos voxne er knoglen ogsaa sjælden.

Af disse 5 accessoriske knogler er der kun 1, der kan phylogenetisk forklares, og det er *os paracuneiforme*, idet det findes saavel hos andre hvirveldyr (embryologisk og hos udvoxede) som i den primitive tetrapodefod; her svarer det til enten centrale *præhallucis* eller tarsale *præhallucis*. At jeg har fundet anlægget saa meget hyppigere hos embryoner, end hvad tilfældet er af fundet af knoglen hos voksne, maa formentlig skyldes, at anlægget enten atter forsvinder eller ikke forbener.

Calcaneus accessorius, *os interphalangeale* og *os subfibulare* er kun fundet hos mennesket; de er ikke fundet embryologisk hos andre hvirveldyr, og findes ej heller i den primitive tetrapodefod. Disse accessoriske knogler kan derfor betragtes som medfødte anomalier.

Os cuneiforme I bipartitum er embryologisk kun paavist hos mennesket; hos udvoxede dyr skal det — foruden hos mennesket — være fundet en enkelt gang hos en pungrotte og et gnavepindsvin. Hos andre hvirveldyr er det ikke fundet, og i den primitive tetrapodefod findes det heller ikke. Phylogenetisk kan det derfor ikke forklares. Men hvordan det skal forklares er usikkert, rimeligst vel som en medfødt anomali.

Endelig skal jeg omtale, at andre forfattere angiver at have fundet *os trigonum* og *os Vesalianum* som selvstændig hyalinbruskanlæg hos menneskelige embryoner.

Os trigonum: som allerede omtalt har jeg aldrig embryologisk fundet denne knogle som selvstændigt hyalinbruskanlæg hos mennesket, skønt den hos voksne findes i 7—10 %. Allerede dette gør, at jeg i høj grad maa betvivle andre forfatteres embryologiske fund hos mennesker af selvstændigt anlæg for *os trigonum*. Gennemgaar man undersøgelserne nøje, staar de heller ikke for kritik. Jeg mener derfor ikke, at *os trigonum* er paavist embryologisk hos mennesket, og jeg mener heller ikke, at der findes et til det svarende primitivt tetrapodefods element.

Os Vesalianum: har jeg ikke fundet embryologisk, det var heller ikke at vente, da det hos voksne findes saare, saare sjældent. En enkelt forfatter har imidlertid et fund fra et nyfødt — desværre misdannet — barn. Efter de sammenlignende embryologiske undersøgelser indenfor hvirveldyrene og efter den primitive tetrapodefods opbygning, vil jeg mene, at *os Vesalianum* kan phylogenetisk forklares, nemlig som det primitive element: tarsale 5 (muligvis tarsale 6 = *postminimus*).

Resultat: selvstændige hyalinbruskpræformede accessoriske knogler hos mennesket kan — alt efter omstændighederne — forklares som phylogenetiske dannelser, neogenetiske dannelser eller tilfældige anomalier.

Fjerde kapitel, diskussion II: Fra visse sider hævdes det, at inkonstante ossificationscentra indenfor eet hyalinbruskanlæg i mange tilfælde giver et fingerpeg om den paagældende dels oprindelige selvstændighed. Med andre ord, saafremt der paa stedet for en accessorisk knogle findes et inkonstant ossificationscentrum, udelukker den manglende embryologiske paavisning af et til den accessoriske knogle svarende hyalinbruskanlæg ikke, at den paagældende accessoriske knogle oprindeligt kan have været selvstændig (hvad enten anlægget saa har været phylogenetisk, neogenetisk eller anomalt).

For nu at kunne afgøre om de accessoriske knogler kan være betinget af tilstedeværelsen af inkonstante ossificationscentre, er det nødvendigt at sammenstille, hvad man ved om inkonstante ossificationscentras tilstedeværelse i foden. Dette er derfor gjort paa basis af literaturen, og yderligere er der suppleret med angivelser for en række pattedyr.

Ved nu at sammenholde de forskellige accessoriske knoglers beliggenhed med de inkonstante ossificationscentras, finder man, at følgende accessoriske knoglers plads kan svare til inkonstante ossificationscentras, og derfor maaske forklares ved disse:

calcaneus accessorius, os cuneiforme I bipartitum, os cuneo-metatarsale I plantare, os naviculare bipartitum, os sesamoideum partitum metatarso-phalangeale, os subfibulare, os subtibiale, os sustentaculi proprium, os talo-naviculare dorsale, os tibiale, os trigonum, os tuberis calcanei og os Vesalianum.

Af disse accessoriske knogler har følgende 4 en beliggenhed, der kan svare til elementer i den primitive tetrapodefod: *os naviculare bipartitum, os subtibiale, os tibiale og os Vesalianum*. Dette vil atter sige, at skylder disse 4 accessoriske knogler deres existens tilstedeværelsen af inkonstante ossificationscentra, vil disse centra kunne phylogenetisk forklares.

Hvad de øvrige nævnte 9 accessoriske knogler angaar, kan man kun sige, at saafremt de skyldes tilstedeværelsen af inkonstante ossificationscentra, kan disse centra skyldes saavel

oprindelige, selvstændige hyalinbruskanlæg (neogenetiske eller anomale) som secundære ossificationscentra opstaaet af ukendt aarsag, uafhængigt af tidligere selvstændige anlæg.

En absolut forudsætning, for at inkonstante ossificationscentra overhovedet skal kunne forklare accessoriske knoglers tilstedeværelse, er imidlertid, at disse centra ikke tilsmelter det øvrige knogleanlæg. Herved kommer man ind paa spørgsmaalet persisterende epiphyser og coalescence. Udfra litteraturen føres der sandsynlighedsbevis for, at den epiphysære proces er den normale udvikling for det inkonstante ossificationscentrum, og den fører til synostose samtidig med væxtens afslutten, mens den coalescære proces er patologisk og ofte ikke fører til synostose. Aarsagen til coalescence maa tilskrives regressive forandringer i brusken, foraarsaget af ufysiologiske belastninger.

Resultat: inkonstante ossificationscentra maa anses for at kunne være aarsag til accessoriske knoglers tilstedeværelse. De inkonstante ossificationscentra maa i visse tilfælde formodes at være sidste rester af oprindelige selvstændige knogleanlæg, hvad enten disse anlæg saa er phylogenetiske, neogenetiske eller anomale. I andre tilfælde maa disse centra betragtes som foreteelser opstaaet uafhængigt af tidligere selvstændige anlæg.

Fjerde kapitel, diskussion III: Udover de allerede anførte aarsager til accessoriske knogler — selvstændige hyalinbruskanlæg og inkonstante ossificationscentra — maa der imidlertid ogsaa findes andre forklaringer; saaledes kan fx. endnu ikke os peroneum fyldestgørende forklares. Fra litteraturen foreligger der nu grundige undersøgelser, der godtgør, at os peroneum er en seneknogle, i. e. en secundær knogle, dannet postnalt som svar paa ydre lokaliserede irritamenter.

Ogsaa for os tibiale foreligger lignende undersøgelser, førende til samme resultat.

Resultat: visse accessoriske knogler kan forklares som seneknogler, i. e. dannelser opstaaet postnalt som svar paa ydre irritamenter.

Fjerde kapitel, diskussion IV: At en række patologiske lidelser kan give anledning til dannelsen af frie selvstændige knogler, er sikkert og vist (jvnf. fx. osteochondrosis dissecans eller

chondromatosis). De herved fremkomne selvstændige knogler falder udenfor min definition paa accessoriske knogler. Men der er sikkert ikke tvivl om, at mange accessoriske knogler skyldes patologiske lidelser, hvis natur ikke sikkert kan erkendes (her tænkes først og fremmest paa gamle pseudartrosiske detaillefracturer). Det er derfor kun rimeligt at afslutte dette arbejde med en omtale af de lidelser, der kan give anledning til dannelsen af frie selvstændige knogler. Disse patologiske lidelser har jeg inddelt i 3 grupper, nemlig lidelser i forbindelse med A) knoglesystemet, B) ledapparatet og C) bløddelene. Lidelserne henregnet til disse 3 grupper skal nævnes:

ad A: fracturer, infectioner, aseptiske knoglenekroser og lokaliserede knoglefortætninger.

ad B: fracturer, artroser, artromer, osteochondrosis dissecans.

ad C: traumatiske bløddelslæsioner, myositis ossificans, calcinosis, ostoma cutis, chondromatosis, karforkalkninger, dystrofiske forkalkninger og forbeninger, forkalkede parasitter og fremmedlegemer.

Resultat: accessoriske knogler kan skyldes ikke erkendte patologiske lidelser.

KONKLUSIONER

En accessorisk knogle kan skyldes:

1. *Et selvstændigt hyalinbruskanlæg og dette kan igen være phylogenetisk, neogenetisk eller anomalt.*

2. *En coalescær proces for et inkonstant ossificationscentrum, dette kan igen skyldes saavel oprindeligt selvstændigt hyalinbruskanlæg (phylogenetisk, neogenetisk eller anomalt) som secundært ossificationscentrum opstaaet af ukendt aarsag, men uafhængigt af tidligere selvstændighed.*

3. *En seneknogle, i. e. en postnatal dannelse opstaaet paa grund af ydre lokaliserede irritamenter.*

4. *En ikke erkendt patologisk lidelse, der tænkes her først og fremmest paa en gammel pseudartrosisk detaillefractur.*

Yderligere maa det pointeres, at een og samme accessoriske knogle hos forskellige individer godt kan have forskellig genese.

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